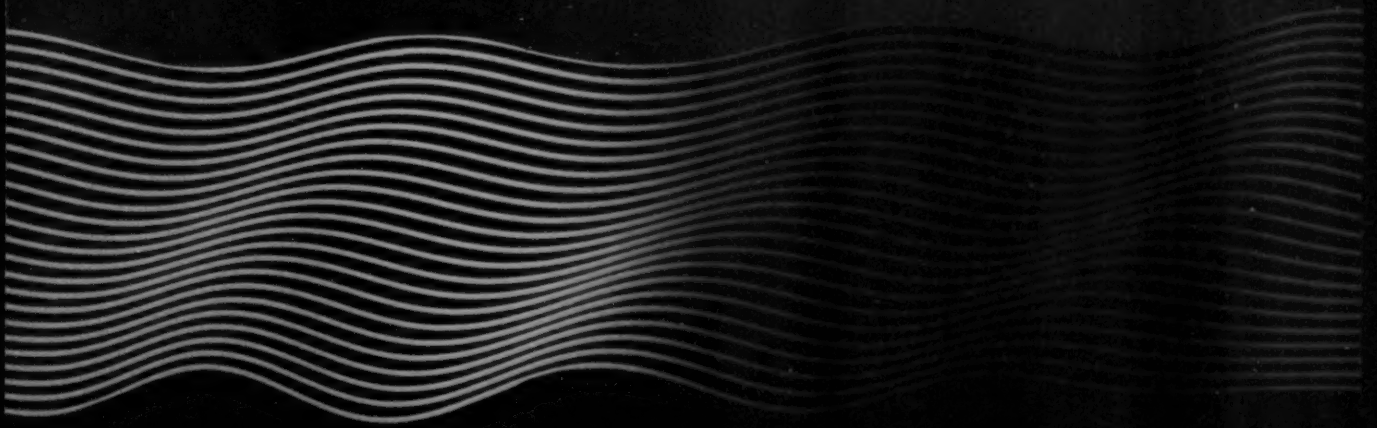
National Research Council Canada

Conseil national de recherches Canada

NRC · CNRC

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques



ISSN 0706-652X / CJFSDX 54(5) 987–1210 (1997)

The *Canadian Journal of Fisheries and Aquatic Sciences*, previously published as *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937, and *Journal of the Fisheries Research Board of Canada* 1938–1979, is issued monthly to form annual volumes of 12 numbers plus supplements.

Editorial policy: The *Journal* publishes original research articles, critical reviews, perspectives (essays of opinion or hypothesis), and comments. Papers may concern cells, organisms, populations, ecosystems, or processes that affect aquatic production systems, and they should lead to identifiable conclusions or synthesis, which variously may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of fisheries and aquatic sciences. They should demonstrate clearly a contribution to knowledge beyond the confirmation state. Originality should relate to more than the particular (a certain year, place, taxon, or chemical compound) such that existing understanding is reformulated or extended.

Manuscripts for publication should be submitted to **Dr. D.G. Cook**, Canadian Journal of Fisheries and Aquatic Sciences, NRC Research Press, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada (613-993-2209; fax: 613-952-7656; e-mail: journal.cjfas@nrc.ca).

Submissions in either English or French are acceptable. The information must be original, that is, not copyrighted, published, or submitted elsewhere except in abstract form or unless by written consent of the Editor. NRC accepts no responsibility for statements or opinions expressed by a contributor. Acceptance of an advertisement, announcement, or other material does not imply endorsement by either the *Journal*'s Editors or NRC. The use of proprietary names does not imply endorsement of the product or company.

Correspondence concerning accepted manuscripts and corrected proofs should be sent to NRC Research Press, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada.

Instructions to Authors are published once a year in the first issue of each volume. Copies are available from NRC Research Press or from our Web site. The **Publication Policy** of NRC Research Press is also available at our Web site:
http://www.nrc.ca/cisti/journals/rj.html

Microfilm: Issues from 1934 through the current volume can be purchased on 16- or 35-mm microfilm. Photocopies of individual articles or issues can be purchased from University Microfilms International, 330 North Zeeb Road, Ann Arbor, MI 48106, U.S.A.

U.S. periodical postage paid at Champlain, N.Y., and at additional mailing offices. Attention U.S. POSTMASTER: Send address changes to **Canadian Journal of Fisheries and Aquatic Sciences**, c/o USACAN Media Distribution Center, P.O. Box 2888, Plattsburg, NY 12901, U.S.A.

Publié sans interruption depuis 1901, le *Journal canadien des sciences halieutiques et aquatiques* a paru sous plusieurs titres : *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937, et *Journal of the Fisheries Research Board of Canada* 1938–1979. Le *Journal* paraît tous les mois, formant ainsi un volume de 12 numéros, et offre en plus jusqu'à deux suppléments par année.

Politique de rédaction : Le journal publie des articles fondés sur une recherche originale, des critiques, des essais portant sur une opinion ou une hypothèse (perspectives) et des commentaires. Les textes peuvent avoir trait aux cellules, aux organismes, aux populations, aux écosystèmes ou aux processus qui influent sur les systèmes de production aquatique. Ils doivent aboutir à des conclusions ou synthèses précises qui, de diverse façons, peuvent accroître, modifier, remettre en question ou réorienter le bagage actuel de connaissances et perceptions dans une discipline donnée des sciences aquatiques. Ils doivent clairement démontrer qu'ils contribuent aux connaissances en faisant plus de corroborer des faits. L'originalité doit dépasser le caractère particulier (une année, un endroit, un taxon ou un composé chimique donnée) et tenir à une épuration ou une reformulation des connaissances actuelles.

Les auteurs doivent adresser leurs **manuscrits** à **D.G. Cook**, Journal canadien des sciences halieutiques et aquatiques, Presses scientifiques du CNRC, Conseil national de recherches du Canada, Ottawa, ON K1A 0R6, Canada (613-993-2209); télécopieur : 613-952-7656; courrier électronique : journal.cjfas@nrc.ca).

Les contributions peuvent être en anglais ou en français. Elles doivent être originales, c.-à.-d. qu'elles ne doivent pas avoir fait l'objet d'un copyright, avoir été publiées ou soumises ailleurs, sauf sous forme abrégée ou avec le consentement du rédacteur. Le CNRC ne se tient en aucune façon responsable des opinions exprimées par un collaborateur ou des déclarations qui pourrait faire ce dernier. La publication d'annonces publicitaires, d'avis et autres n'implique pas l'endossement de leur contenu par les directeurs du *Journal* ou du CNRC. L'utilisation des noms de marques de commerce ne signifie aucunement une sanction du produit en question ou de la compagnie qui le fabrique.

La correspondance ayant trait aux manuscrits acceptés et les **épreuves corrigés** doivent être envoyées aux Presses scientifiques du CNRC, Conseil national de recherches du Canada, Ottawa, ON K1A 0R6, Canada.

Recommandations aux auteurs sont publiés une fois par année dans le premier numéro de chaque volume. Des copies, ainsi que la **Politique de publication**, sont disponibles auprès des Presses scientifiques du CNRC ou au site Web :
http://www.nrc.ca/cisti/journals/rj.html

Microfilms : On peut acheter sur microfilms de 16 ou 35 mm tous les numéros depuis 1934. Des photocopies d'articles ou de numéros individuels sont aussi en vente auprès de University Microfilms International, 330 North Zeeb Road, Ann Arbor, MI 48106, É.-U.

This journal is indexed or abstracted in / Ce journal est signalé ou résumé dans
Aquatic Sciences and Fisheries Abstracts, Biological & Agricultural Index, CAB Abstracts (Centre for Agriculture and Biosciences), Chemical Abstracts, Current Awareness in Biological Sciences, Current Contents, FAO Freshwater and Aquaculture Contents Tables, FAO Marine Science Contents Tables, GEOBASE – Geo Abstracts, Meteorological and Geoastrophysical Abstracts, Oceanic Abstracts, Science Citation Index, Biological Abstracts, Environment Abstracts, Environmental Periodicals Bibliography, GEOREF, Life Sciences Collection, and PASCAL Database

In this issue of the Canadian Journal of Fisheries and Aquatic Sciences there are two challenging Perspectives that may be interpreted as critical of the Department of Fisheries and Oceans. These articles were subjected to the same refereeing and editorial review procedures as any other submission to the journal. The authors were asked for their permission to provide advance copies of the Perspectives to DFO so that DFO could respond in the same issue. As is their right according to the editorial policy of the CJFAS, the authors declined to do so. A response from the Department on the scientific issues raised is anticipated in the June issue of the Journal.

NRC Research Press

Le présent numéro du Journal canadien des sciences halieutiques et aquatiques rend compte de deux perspectives qui seront peut-être perçues comme condamnant au ministère des Pêches et des Océans. Je tiens à souligner que ces articles ont bel et bien été soumis à l'exercice d'examen par les pairs et d'examen par la rédaction, au même titre que tout article présenté au Journal. On a demandé la permission aux auteurs de faire connaître ces perspectives au MPO avant la publication de façon à ce que le Ministère puisse donner la réplique dans le même numéro. Comme le leur permet la politique éditoriale du Journal, les auteurs ont décliné cette offre. Nous espérons donc vous offrir la répartie du Ministère dans le numéro de juin.

Presses scientifique du CNRC

Volume 54, Number 5, May 1997

Canadian Journal of Fisheries and Aquatic Sciences

Published by the National Research Council of Canada

Volume 54, numéro 5, mai 1997

Journal canadien des sciences halieutiques et aquatiques

Publié par le Conseil national de recherches du Canada

Editor / directeur scientifique D.G. Cook
Assistant to the Editor / adjointe au directeur scientifique **M.M. Milne**
Consulting Editor / rédacteur-conseil **P.E.K. Symons** (Victoria, B.C.)
Consulting Editor / rédactrice-conseil **N. Moir** (Nepean, Ont.)

Editorial Board / conseil de rédaction

S.E. Campana, *DFO/MPO, Dartmouth*
E.M.P. Chadwick, *DFO/MPO, Moncton*
L.M. Dickie, *DFO/MPO, Dartmouth*
G.S. Jamieson, *DFO/MPO, Nanaimo*
J.R.M. Kelso, *DFO/MPO, Sault Ste. Marie*
K.R. Munkittrick, *DoE/MdE, Burlington*
J.D. Neilson, *DFO/MPO, St. Andrews*
D.L.G. Noakes, University of Guelph
L.S. Parsons, *DFO/MPO, Ottawa*
R.M. Peterman, *Simon Fraser University*
R.D. Robarts, *DoE/MdE, Saskatoon*
J.C. Roff, *University of Guelph*
D.M. Rosenberg, *DFO/MPO, Winnipeg*
P. Schwinghamer, *DFO/MPO, St. John's*
(Deputy editor / rédacteur adjoint)
C.J. Walters, *University of British Columbia*
W.G. Warren, *DFO/MPO, St. John's*
N.H.F. Watson, *DFO/MPO, Halifax*

NRC Research Press / Presses scientifiques du CNRC
Editor-in-chief / directeur général **Bruce P. Dancik**
Assistant Editor-in-chief / directeur général adjoint **Iain E.P. Taylor**

Journals Program / Programme des revues
(Fax / télécopieur : 613-952-7656; e-mail / courrier électronique : research.journals@nrc.ca;
URL: http://www.nrc.ca/cisti/journals/)
Director / directrice **Aldyth Holmes**
Business Manager / gestionnaire des affaires **Paul McClymont**
Manager, Journals Program / gestionnaire, Programme des revues **Susan R. Strahlendorf**
Senior Publication Officer / agent principal de publication **Mike Boroczki**
Publication Officers / agentes de publication **Jennifer Douglas (613-993-0368), Jennifer McColl (613-993-4500)**
Publication Officer (French manuscripts) / agente de publication (manuscrits français) **Ginette Fortier (613-993-9117)**
Advertising / annonces publicitaires **Judy Heyman (613-993-0151)**
Reprints / tirés à part **Judy Heyman (613-993-0151)**
Subscriptions / abonnements **Helen Goulet (613-993-9084)**

© National Research Council of Canada 1997. World rights reserved.

No part of this publication may be reproduced, stored, or transmitted in any form or by any means, without the written permission of the publisher, except as stated below.

The National Research Council of Canada grants **permission*** to individuals to make single copies of articles for personal use. Any person may reproduce short excerpts from articles in the journal for any purpose that respects the moral rights of authors, provided that the source is fully acknowledged. As a courtesy, the consent of authors of such material should be obtained directly from the author.

Authorization to reproduce items for other than personal use, as stated above, is granted by the National Research Council of Canada provided that the copyright fee of $7.00 per copy is paid directly to the Copyright Clearance Center (CCC) Transactional Reporting Service, 21 Congress Street, Salem, MA 01970, U.S.A. 0706-652x/97 $7.00 + 0.00.

*The above permission does not extend to other kinds of copying, such as copying for general distribution, for advertising, or promotional purposes, for creating new collective works, or for resale. For such copying, arrangements must be made with the publisher, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada.

© Conseil national de recherches du Canada 1997. Tous droits réservés.

Il est interdit de reproduire, de sauvegarder ou de transmettre quelque partie de la présente publication dans quelque format ou de quelque façon sans le consentement écrit de l'éditeur, à l'exception des conditions suivantes.

Le Conseil national de recherches du Canada accorde aux particuliers le droit de faire des copies individuelles pour leur usage personnel. Toute personne peut reproduire de courts extraits des articles de la Revue pour autant que les droits moraux de l'auteur soient respectés et que la mention de provenance soit clairement indiquée. Il est de convenance de demander le consentement de l'auteur avant de faire mention de son travail.

On obtiendra l'autorisation de reproduire des articles à d'autres fins que l'usage personnel (tel qu'on l'a décrit ci-dessus) auprès du Conseil national de recherches du Canada pour autant que des redevances de droits d'auteurs de 7,00 $/copie soient versées au Copyright Clearance Center (CCC) Transactional Reporting Service, 21 Congress Street, Salem, MA 01970, U.S.A. 0706-652x/97 7,00 $ + 0,00.

*La permission ci-dessus ne s'applique pas à la reproduction à grande échelle, telle que la reproduction aux fins de distribution générale, publicitaire ou promotionnelle, de compilation de nouveaux ouvrages collectifs ou de revente. Dans de tels cas, il faudra ratifier une entente particulière avec l'éditeur, le Conseil national de recherches du Canada, Ottawa, ON K1A 0R6, Canada.

Subscription information

The *Canadian Journal of Fisheries and Aquatic Sciences* (ISSN 0706-652X) is published monthly by the National Research Council of Canada. 1997 annual subscription rates (second class postage) for Canada are $461CAN institutional and $157CAN personal, for US & foreign $461US institutional and $167US personal. For air mail add $150US to foreign rate. Canadian customers please include 7% GST (business no. 12149 1807 RT 0275). In Quebec please add a further 6.5% QST to the total price including GST (QST no. 1006178088). Subscriptions are entered for the calendar year. Remittances should be made payable to the Receiver General for Canada credit NRC. Price for regular single issues: institutional, $60.00; personal, $25.00. Supplements will be priced separately. Special rates apply to members of Canadian scientific and engineering societies if they subscribe through their respective societies.

There are no refunds on cancelled subscriptions once delivery has begun. Claims for missing issues should be made within four months (N. America) or six months (outside N. America) following the date of publication. The publisher expects to supply missing issues only when losses have occurred in transit and when the reserve stock will permit. For change of address and subscription enquiries: Subscription Office, NRC Research Press, National Research Council Canada, Ottawa, ON K1A 0R6, Canada; tel: 613-993-9084; fax: 613-952-7656; e-mail: research.journals@nrc.ca.

Microform backfiles are available from UMI, P.O. Box 1346, Ann Arbor, MI 48106-1346, U.S.A., and Micromedia Ltd., 20 Victoria St., Toronto, ON M5C 2N8, Canada.

Renseignements sur l'abonnement

Journal canadien des sciences halieutiques et aquatiques (ISSN 0706-652X) est une publication mensuelle du Conseil national de recherches du Canada. Le prix de l'abonnement annuel au Canada (courrier de deuxième classe) est de 461 $CAN pour les organismes et de 157 $CAN pour les particuliers. À l'étranger (y compris les É.-U.), le prix de l'abonnement est de 461 $US pour les organismes et de 167 $US pour les particuliers. L'expédition par avion exige des frais de 150 $US en sus du prix d'abonnement à l'étranger. Les clients du Canada doivent ajouter la TPS de 7% (numéro d'entreprise 12149 1807 RT 0275). Au Québec, il faut ajouter la TVQ de 6,5% au prix total, TPS comprise (n° de TVQ 1006178088). Les abonnements sont pour l'année civile. Tout paiement doit être adressé au Receveur général du Canada, crédit du CNRC. Le prix par numéro est de 60 $ pour les organismes et de 25 $ pour les particuliers. Le prix des hors-série varie. Les membres des sociétés canadiennes de sciences et de génie bénéficient de taux préférentiels en s'abonnant via leurs sociétés respectives.

Aucun remboursement ne sera accordé ni aucune annulation acceptée une fois que les livraisons auront commencé. Les réclamations de numéros manquants devront être soumises dans les quatre mois (Amérique du Nord) ou dans les six mois (à l'extérieur de l'Amérique du Nord) suivant la date de publication. L'éditeur ne fournira de numéros manquants que si le document a été perdu pendant l'expédition et que si le stock le permet. Adressez tout changement d'adresse ou toute question quant à l'abonnement au : Bureau des abonnements, Presses scientifiques du CNRC, Conseil national de recherches Canada, Ottawa, ON K1A 0R6, Canada; téléphone : 613-993-9084; télécopieur : 613-952-7656; courrier électronique : research.journals@nrc.ca.

On peut obtenir les fichiers rétrospectifs sur **microforme** auprès de UMI, P.O. Box 1346, Ann Arbor, MI 48106-1346, É.-U., et auprès de Micromedia Ltée, 20 rue Victoria, Toronto, ON M5C 2N8, Canada.

EDITORIAL / ÉDITORIAL

Two important and challenging perspectives appear in this issue of the *Canadian Journal of Fisheries and Aquatic Sciences* (CJFAS). Both examine problems within Canadian regulatory institutions that may impede effective and proper management of the resources under their charge. Both, in my opinion, deserve careful and dispassionate consideration by politicians, bureaucrats, scientists, and the host of publics with special interests in fisheries and aquatic resources, regardless of nationality.

Kerr and Ryder (1997) draw a compelling parallel between the many decades of radical anthropogenic alteration to the Laurentian Great Lakes ecosystem and the devastating changes now occurring in northwestern Atlantic fisheries. They analyse the disciplinary, institutional, and jurisdictional barriers that existed in the Great Lakes basin both to the scientific understanding of the nature of change and to the implementation of effective remedial action. Their perspective on common problems seen first in the Great Lakes and now in Atlantic Canada leads to a cogent plea that the Canadian Department of Fisheries and Oceans (DFO) must truly understand and implement a cooperative "ecosystem approach" to management: for unless DFO can benefit from the painful lessons of history, the prognosis for traditional Atlantic fisheries could be very gloomy indeed.

Hutchings et al. (1997) approach the difficult question of government manipulation of the science and scientists under its direct control. By documenting events surrounding stock assessments of Atlantic cod and negotiations concerning flow regimes in the Nechako River, British Columbia, they demonstrate a tendency for DFO to suppress scientific facts and opinions that do not conform either to current departmental orthodoxy or to political expediency. This disturbing pattern lends great strength to their argument that a politically independent organization (reminiscent of the late, lamented Fisheries Research Board of Canada (FRB)) is required to provide the difficult, vital link between scientific research and resource management.

Although perhaps the majority of our readers will appreciate the grave, general nature of the problems addressed in these two Perspectives, I believe it inevitable that some may attempt to attack either the messages or the messengers, and that some may ask why CJFAS would deem it necessary to expose dirty Canadian laundry to an international audience. A brief but sufficient response to these potential critics is my affirmation (1) that both Perspectives were accepted after being subjected to the same stringent peer review procedures as apply to all submissions (and to more editorial agonizing than many) and (2) that the review process, which in both cases involved American and Canadian referees, confirmed the international importance of the subjects discussed. The incoming Editors will, I understand, follow CJFAS's traditional policy of welcoming substantive commentary on the Perspectives for consideration as either independent contributions or Letters to the Editor.

For those fortunate enough to have escaped bureaucratic influences, I feel obliged to respond more fully by outlining

Dans la présente livraison du *Journal canadien des sciences halieutiques et aquatiques*, nous vous offrons deux perspectives importantes qui vous inviteront à réflexion. Elles abordent les défis qui se dressent devant les organismes de réglementation responsables et qui nuisent à la gestion efficace et éclairée des ressources. Je crois qu'elles doivent soulever un débat international désintéressé et attentif chez les politiques, les bureaucrates, les scientifiques et les différents groupes s'intéressant aux pêcheries et aux ressources aquatiques.

Kerr et Ryder (1997) comparent les décennies d'altération anthropique profonde de l'écosystème des Grands Lacs laurentiens à l'effondrement dévastateur que connaît actuellement l'industrie poissonnière dans le sud-ouest de l'Atlantique. Ils analysent les barrières érigées par les écoles de pensée, les institutions et les conflits de compétence qui ont entravé l'élargissement des connaissances scientifiques sur les changements que subissait le bassin des Grands Lacs et les interventions correctives. Ce parallèle entre les Grands Lacs et le Canada Atlantique les amène à insister auprès du ministère des Pêches et des Océans pour qu'il adopte une gestion coopérative fondée sur les écosystèmes à défaut de quoi l'avenir de l'industrie de la pêche traditionnelle dans le Canada Atlantique pourrait être très incertain.

Hutchings et ses collaborateurs (1997) abordent la question différemment. Ils y voient plutôt une manipulation des données et des scientifiques par le gouvernement. Après avoir décrit les événements entourant l'évaluation des populations de morue ainsi que les négociations portant sur la régularisation des débits de la rivière Nechako, ils avancent que le ministère des Pêches et des Océans est parfois porté à étouffer les faits et les opinions scientifiques par simple opportunisme politique ou parce qu'ils s'éloignent de la ligne de pensée ministérielle. Cette situation troublante appelle la mise sur pied d'un organisme apolitique à l'instar du défunt Conseil de recherches sur les pêcheries afin de nouer un lien délicat et essentiel entre la recherche scientifique et la gestion des ressources.

La plupart de nos lecteurs comprendront sûrement la gravité des préoccupations soulevées par ces auteurs, mais nous savons également que certains décrieront le sujet ou nous condamnerons pour avoir étalé nos problèmes sur la scène internationale. À ces personnes, je dis ce qui suit : en premier lieu, nous avons accueilli les deux perspectives après les avoir soumises à la même appréciation rigoureuse que les autres articles (et je dois dire après une critique éditorialiste plus que sévère) et en deuxième lieu, l'appréciation exécutée par des pairs américains et canadiens a confirmé la pertinence internationale des sujets traités. Je crois savoir que les nouveaux rédacteurs respecteront la politique actuelle du Journal et accueilleront les commentaires de fond sur les Perspectives qui lui sont transmis sous forme d'articles ou de lettres à la Rédaction.

Je veux dire à ceux qui se sont libérés du joug des influences bureaucratiques que je crois sincèrement que le Journal se devait de publier ces perspectives. Les deux essais

my personal conviction that CJFAS had a moral obligation to the community to publish these Perspectives. Both works probe issues at the very heart of CJFAS's role in the community, which according to one objective view is to provide "the major communication channel between the more applied world of fisheries research and the basic research venues of marine biology and oceanography" (McCain 1994, p. 26). Perusal of almost any recent issue of *Nature* (*London*) or *Science* (*Washington, D.C.*) will support the assertion that social, political, and bureaucratic influences on scientific affairs have become increasingly pervasive in the last two to three decades, as will the existence of scholarly journals devoted to social dimensions of science and technology (e.g., *Social Studies of Science*, founded 1971; *Science, Technology & Human Values*, founded 1975). However, the nature of the least desirable influences on science renders them inherently dangerous, and intrinsically difficult to document and analyse. Thus, when such matters are discussed in a scholarly fashion, I believe that broad exposure and candid debate are the only healthy outcomes.

In my view, it is a short step from the type of suppression described by Hutchings et al. (1997) and other incidents reported in the news media (e.g., Spears 1991, 1996; *Winnipeg Free Press* 1991; *Globe & Mail* 1996) to censorship of primary scientific publications. I affirm that while CJFAS was published by the communications arm of DFO, an unsuccessful attempt was in fact made to alter a statement in an accepted paper that might have temporarily embarrassed the Department. This was reported (September 1988) to the politically independent Fisheries and Oceans Research Advisory Council (now regrettably disbanded), and such incidents were not repeated; however, an unethical verbal attempt was made in 1994 to subvert the anonymity of the peer review process regarding a paper that displeased DFO. It is my hope that widespread awareness of these problems may tend to reduce the incidence of systemic abuse by placing the community on its guard and perhaps by inducing some bureaucratic caution in matters of scientific information control. The transfer of CJFAS to a new publisher (the National Research Council of Canada (NRC)) in 1993 insulated the editorial office from direct influence by DFO, and the forthcoming transfer of the editorship to Academia should complete this process.

Fortunately, Editors see the best as well as the worst of ethical behaviour in scientific publishing. Individual DFO scientists, who have provided CJFAS sustained support throughout its history with influential papers, excellent reviews, and invaluable editorial assistance, are deservedly among the most respected fisheries and aquatic workers anywhere in the world (Hamilton 1991), as are their academic counterparts (Peters et al. 1996). It has been my great privilege to have interacted with so many of these scientists and those elsewhere in North America, Europe, and Australasia.

I thank most sincerely the community of scholars and general readership of CJFAS; past and present members of our Editorial Board; Consulting Editors P.E.K. Symons and N. Moir, without whom I could not have managed this Journal; P. Burke and the dedicated Publication Officers at NRC; M. Milne, perceptive and indispensable Editorial Assistant extraordinaire; and the many authors, reviewers, and editors who have wished me well for my imminent retirement. I wish the new co-Editors, J.C. Roff and M.M. Ferguson, every possible

touchent à l'essence même de la vocation du Journal qui, selon une opinion désintéressée, est d'être le principal lien entre la recherche appliquée sur les pêches et la recherche fondamentale en biologie marine et en océanographie (McCain 1994, p. 26). Les articles publiés récemment dans *Nature* (*Londres*) et *Science* (*Washington, D.C.*) tout comme ceux dans des publications savantes s'intéressant aux dimensions sociales de la science et de la technologie (Social Studies of Science lancée en 1971, Science, Technology & Human Values, lancée en 1975) opinent également que les volets sociaux, politiques et bureaucratiques exercent une influence plus grande et plus profonde sur les sciences depuis les deux ou trois dernières décennies. Cependant, l'essence même de ces influences néfastes en fait des réalités dangereuses indescriptibles et impénétrables. Donc, lorsque nous abordons savamment ces sujets, je crois qu'un vaste éclatement et un franc débat sont les seules saines issues possibles.

Je suis d'avis que la dissimulation dont parle Hutchings et ses collaborateurs (1997) et les autres incidents décrits dans les médias (Spears, 1991, 1996; Winnipeg Free Press 1991; Globe & Mail 1996) peuvent mener à la censure des publications scientifiques de premier plan. Je peux vous affirmer maintenant que lorsque le Journal était publié par les Communications du ministère des Pêches et des Océans, on a tenté en vain d'altérer un avis dans un rapport qui aurait pu embarrasser momentanément le Ministère. Cette tentative avait été signalée à l'ex-Conseil de recherches sur les pêcheries en septembre 1988 et il n'y avait pas eu récidive, mais en 1994, on a tenté verbalement de miner l'anonymat du processus d'appréciation d'un rapport qui déplaisait au ministère. J'espère qu'une sensibilisation plus vaste à ces problèmes et la mise en garde donnée à la collectivité scientifique réduiront les abus et inciteront la bureaucratie à la prudence dans les tentatives de contrôle de l'information scientifique. Le passage de la publication du Journal au Conseil national de recherches du Canada en 1993 a libéré la Rédaction de la férule du ministère et l'affranchissement sera entier lorsque sous peu la responsabilité éditoriale relèvera d'universitaires.

Le personnel éditorial ne voit pas que les mauvais côtés de l'édition scientifique. Les scientifiques du ministère qui ont toujours fourni un appui indéfectible au Journal au fil des ans en lui communiquant des articles déterminants, des recensions de grande qualité et une aide éditoriale inestimable comptent, tout comme leurs pairs universitaires, parmi les experts des milieux aquatiques et halieutiques les plus renommés à l'échelle mondiale (Hamilton 1991). Je suis très honoré d'avoir pu échanger avec ces scientifiques et ceux de l'Amérique du Nord, de l'Europe et de l'Australie.

Je tiens à remercier les universitaires et nos lecteurs, les membres et ex-membres de notre comité de rédaction ainsi que les conseillers éditoriaux P.E.K. Symons et N. Moir sans qui je n'aurais pu accomplir ma tâche. Je voudrais également souligner l'appui de P. Burke du Bureau des publications au CNRC ainsi que la perspicace et indispensable M. Milne, adjointe à la rédaction. En dernier lieu, il y a les nombreux collaborateurs, recenseurs et rédacteurs qui m'ont souhaité une retraite bien remplie. Je souhaite à la nouvelle équipe de rédaction formée de J.C. Roff et M.M. Ferguson les meilleurs des succès dans l'avancement des politiques et de la vocation du Journal et l'enrichissement de sa réputation. J'espère que

success for advancing the *Journal*'s policies and procedures, and for sustaining the best of its reputation; I hope that the community will extend to them the support, trust, and understanding that my predecessors and I have enjoyed.

vous leur donnerez l'appui, la confiance et la compréhension que vous m'avez démontrés ainsi qu'à mes prédécesseurs.

David G. Cook
Editor/directeur scientifique

References / Bibliographie

Globe & Mail. 1996. Canadian quits joint commission [p. A1] and Canadian quits over suppressed report [p. A7]. Globe & Mail, Toronto, Ont., 10 Sept. 1996.

Hamilton, A.L. 1991. The Stockholm Water Prize and the Experimental Lakes Area — Guest editorial. Can. J. Fish. Aquat. Sci. **48**: 1132–1135.

Hutchings, J.A., Walters, C., and Haedrich, R.L. 1997. Is scientific inquiry incompatible with government information control? Can. J. Fish. Aquat. Sci. **54**: 1198–1210.

Kerr, S.R., and Ryder, R.A. 1997. The Laurentian Great Lakes experience: a prognosis for the fisheries of Atlantic Canada. Can. J. Fish. Aquat. Sci. **54**: 1190–1197.

McCain, K.W. 1994. Islands in the stream: mapping the fisheries and aquatic sciences literatures. Fisheries (Bethesda), **19**(10): 20–27.

Peters, R.H., Ball, G.E., Carignan, R., Hebert, P.D.N., and Prepas, E.E. 1996. An assessment of research in evolution and ecology supported by the Natural Sciences and Engineering Research Council of Canada. Can. J. Fish. Aquat. Sci. **53**: 670–680.

Spears, T. 1991. Bureaucracy puts 'muzzle' on science, says ecologist. The Ottawa Citizen, Ottawa, Ont., 2 Oct. 1991. p. A12.

Spears, T. 1996. Canadian quits top job with pollution watchdog. The Ottawa Citizen, Ottawa, Ont., 11 Sept. 1996. p. A4.

Winnipeg Free Press. 1991. Muzzling an expert. Winnipeg Free Press, Winnipeg, Man., 16 Oct. 1991. p. A6.

Origin of the relation between K and L_{inf} and synthesis of relations among life history parameters

A.L. Jensen

Abstract: Four patterns occur in growth and mortality parameters across species of fish. Three of these relations, $Mx_{\text{m}} = 1.65$, $M = 1.50K$, and $L(x_{\text{m}}) = 0.66L_{\text{inf}}$ where M is natural mortality, x_{m} is age at maturity, $L(x_{\text{m}})$ is length at maturity, and L_{inf} is asymptotic length, were previously shown to result from optimization of the age at maturity. In this study the fourth relation, that between asymptotic size and the growth coefficient, $L_{\text{inf}} = CK^{-h}$, was obtained from a bioenergetic growth equation. A numerical value of $h = 0.33$ was predicted, and this agrees with the observed value. The relation between the growth coefficient K and size L_{inf} results from the limited amount of assimilated food that must be used both for growth and body functions, and the body functions are a function of body size. The four Beverton and Holt invariants, together with the net reproductive rate, relate many life history parameters to a metabolic parameter and mortality.

Résumé : Quatre relations sont observées dans les paramètres de croissance et de mortalité dans les diverses espèces de poissons. On a antérieurement démontré que trois de ces relations, $Mx_{\text{m}} = 1{,}65$, $M = 1{,}50K$ et $L(x_{\text{m}}) = 0{,}66L_{\text{inf}}$ où M est la mortalité naturelle, x_{m} est l'âge à maturité, $L(x_{\text{m}})$ est la longueur à maturité et L_{inf} est une longueur asymptotique, résultaient de l'optimisation de l'âge à maturité. Dans la présente étude, la quatrième relation, celle entre la taille asymptotique et le coefficient de croissance, $L_{\text{inf}} = CK^{-h}$, a été obtenue à partir d'une équation de croissance bioénergétique. Une valeur numérique de $h = 0{,}33$ a été prévue et cette valeur est en accord avec la valeur observée. La relation entre le coefficient de croissance K et la taille L_{inf} résulte de la petite quantité d'aliments assimilés qui doit être utilisée à la fois pour la croissance et les fonctions corporelles, et les fonctions corporelles dépendent de la taille corporelle. Les quatre invariants de Beverton et Holt combinés au taux de reproduction net relient de nombreux paramètres du cycle vital à un paramètre métabolique et à la mortalité.

[Traduit par la Rédaction]

Introduction

Beverton and Holt (1959), Holt (1962), and Beverton (1963) discovered several patterns in growth and mortality parameters across fish species. One pattern was the relation between length at maturity and asymptotic length, a second pattern was the relation between natural mortality and the von Bertalanffy growth coefficient, and a third pattern was the relation between asymptotic length and the growth coefficient. Charnov and Berrigan (1990) noted that the above relations implied a relation between age at maturity and natural mortality. These patterns were reviewed by Cushing (1968), Beverton (1992), and Charnov (1993) and they are of both practical and scientific interest.

Holt (1962) indicated that these invariants could be used to estimate difficult to estimate parameters from more easily estimated parameters, and Pauly (1980) used data for 175 different species to obtain a regression of natural mortality on growth parameters that is useful for estimation of natural mortality from more easily estimated growth parameters. Beverton (1963) and Charnov (1993) suggested that these relations resulted from natural selection and that they were adaptations to maximize the contribution of progeny to future generations. Jensen (1996) obtained the first three of these relations by optimization of the age at maturity in Roff's (1992) fecundity function. The first three relations result from age at maturity occurring when the reproductive biomass of a cohort is maximum.

The relation between asymptotic size and the growth coefficient was not obtained through optimization of the age at maturity, and it does not appear directly related to the three other relations. Charnov (1993) suggested that the relation between asymptotic size and the growth coefficient might occur as the result of a constraint on growth, and in this article, I obtained it from a simple bioenergetic growth equation. A numerical value for the exponent is predicted and compared with values estimated by Charnov (1993). The four Beverton and Holt invariants, together with the net reproductive rate, are used to obtain relations that determine many life history parameters from the metabolic parameters and mortality.

Derivation of the relation between K and L_{inf}

Based on metabolic considerations, Putter (cited in Ursin 1967) assumed that growth in weight could be described as

$$(1)\quad dW/dx = HW^{2/3} - kW$$

where x is age (years), H (grams$^{1/3}$ per year) and k (grams per year) were parameters, and W (grams) was weight. If growth is isometric and specific gravity is constant, then

$$(2)\quad W = qL^3$$

Received January 30, 1996. Accepted October 7, 1996.
J13277

A.L. Jensen. School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI 48109-1115, U.S.A.

Can. J. Fish. Aquat. Sci. **54**: 987–989 (1997)

Table 1. Estimates of parameter *h* for many populations (*n*) of several different species using Pauly's (1978) data.

Species	*n*	*h*
Gadus morhua	49	0.38
Melanogrammus aeglefinus	13	0.59
Merlangius merlangus	91	0.35
Clupea harengus	39	0.20
Sardina pilchardus	18	0.28
Sardinops caerula	19	0.22
Sardinella aurita	13	0.28
Brevoortia tyrannus	43	0.33
Engraulis japonicus	15	0.37
Engraulis encrasicholus	17	0.20
Engraulis mordax	26	0.24

where L is length (centimetres) and q (grams per cubic centimetre) is a parameter. At equilibrium, where $\mathrm{d}W/\mathrm{d}x = 0$ and $W(x) = W_{\mathrm{inf}}$, eq. 1 with $k = 3K$ gives

$$(3) \qquad 3KW_{\mathrm{inf}} = HW_{\mathrm{inf}}^{2/3}$$

where K (per year) is the growth coefficient of the von Bertalanffy growth equation. Substitution of $qL_{\mathrm{inf}}3$ for W_{inf} on the left-hand side of eq. 3 leads to

$$(4) \qquad L_{\mathrm{inf}} = C_1K^{-1/3}$$

where

$$(5) \qquad C_1 = (HW_{\mathrm{inf}}^{2/3}/3q)^{1/3}.$$

Equation 4 is the relation between L_{inf} and K that appears in statistical analyses across species, and it results from relations among metabolic and growth parameters.

Verification of equation 4

If the exponent in the relation between length and weight (eq. 2) is assumed equal to 3, as occurs with isomorphic growth, eq. 4 indicates that in the relation (Beverton and Holt 1959)

$$(6) \qquad L_{\mathrm{inf}} = C_1K^{-h}$$

the parameter h equals 0.33. Simple linear regression estimates of h within several populations of the same species calculated with the data of Pauly (1978) are listed in Table 1, and the average value of h over all species was 0.31, which is close to the predicted value of 0.33.

To confirm that the parameter C_1 is described by eq. 5, C_1 was estimated both directly from metabolic parameters and from the regression of L_{inf} on K. Data for estimation of C_1 from metabolic parameters are available for few species, but Ursin (1979) gave the necessary parameters for plaice (*Pleuronectes platessa*). The parameter estimates $H = 4.049\ \mathrm{g}^{1/3}\cdot\mathrm{yr}^{-1}$, $W_{\mathrm{inf}} = 3.430$ g (for females), and $q = 0.01\ \mathrm{g}\cdot\mathrm{cm}^{-3}$ gave $C_1 = 29.71$. The 15 observations for the family Pleuronectidae given by Pauly (1980) gave $C_1 = 27.46$ in a simple linear regression with h set at –0.33. The two estimates of C_1 are close.

The observed relations between L_{inf} and K obtained by Charnov (1993) applied to limited taxonomic groups, and eq. 5 indicates that C_1 may vary among groups because the parameter C_1 contains asymptotic weight that varies among groups. Equations 4 and 5 together indicate that

$$(7) \qquad L_{\mathrm{inf}}K^{1/3} = C_2W_{\mathrm{inf}}^{0.25}$$

where the new parameter $C_2 = (H/3q)^{1/3}$ contains neither W_{inf} nor L_{inf}. Applying the data of Pauly (1980) for all 175 populations gave $L_{\mathrm{inf}}K^{1/3} = 5.43W_{\mathrm{inf}}0.25$ with $R^2 = 0.89$. The estimated exponent for W_{inf} of 0.25 agrees closely with that of eq. 7. For plaice, the estimated value of C_2, together with the estimate $H = 4.049\ \mathrm{g}^{1/3}\cdot\mathrm{yr}^{-1}$, gives $q = 0.0084\ \mathrm{g}\cdot\mathrm{cm}^{-3}$, which is close to the observed value of $0.01\ \mathrm{g}\cdot\mathrm{cm}^{-3}$, indicating that the estimated value of C_2 also is reasonable.

Discussion

Equation 4 is one of two relations between K and L_{inf} obtainable from growth equations. The second relation is obtained when the equation for growth in length is derived from the weight equation. Differentiation of eq. 2 gives $\mathrm{d}W/\mathrm{d}x = 3qL^2\mathrm{d}L/\mathrm{d}x$, and substitution into the weight equation gives $\mathrm{d}L/\mathrm{d}x = Hq^{-1/3}/3 - kL/3$ (e.g., Ursin 1967). If we let $KL_{\mathrm{inf}} = Hq^{-1/3}/3$ and $K = k/3$, we obtain the von Bertalanffy equation for growth in length $\mathrm{d}L/\mathrm{d}x = K(L_{\mathrm{inf}} - L)$ (e.g., Ursin 1967). In this derivation, KL_{inf} is the initial rate of increase in length, which is constant for a particular growth curve, but this is not the relation that appears in statistical analyses of K and L_{inf} across species.

Equations 4 and 5 indicate that the observed statistical relation between K and L_{inf} across species depends on the term $HW^{2/3}$ in eq. 1, and Ursin's (1967) bioenergetic development of eq. 1 is helpful in understanding the constraint on K and L_{inf}. Growth in weight results from the difference between the amount of energy available for growth and that required for feeding and fasting catabolism. The term $HW^{2/3}$ in the growth equation is the difference between the amount of food assimilated and feeding catabolism. Ursin (1967) gave the ration of an individual fish, $\mathrm{d}R/\mathrm{d}x$, as $\mathrm{d}R/\mathrm{d}x = bfW^{2/3}$ where f is a feeding level that can be modelled with the Ivlev (1961) equation that gives feeding level as a function of available food and b is a coefficient of food consumption that is dependent on temperature and the animal's physiology. The amount of food ingested that is absorbed is $p\mathrm{d}R/\mathrm{d}x$ where p is the proportion absorbed; hence, the amount of assimilated food is $pbfW^{2/3}$. Feeding catabolism includes the energy cost of catching and swallowing food, production of digestive enzymes, production of large molecules from small molecules, and deamination of proteins to be stored as fat (Ursin 1967). Ursin (1967) assumed that feeding catabolism was proportional to the amount of food assimilated, and thus in terms of metabolic parameters the constant C_1 is

$$(8) \qquad C_1 = [(1 - u)pbf\,W_{\mathrm{inf}}^{2/3}/3q]^{1/3}$$

where u is the proportion of assimilated food that is utilized for feeding catabolism. The relation between the growth coefficient K and size L_{inf} results from a limited energy resource; assimilated food must be used for both growth and other body functions, and for a limited energy resource, if the asymptotic length is larger, more assimilated food is required for body maintenance, movement, etc., and less energy is available for growth, and K is smaller.

Many of the observed patterns among life history parameters can be explained in terms of an optimal age at maturity, a limited food resource, a limited ability of organisms to assimilate and utilize food resources, and the necessity of a demographic balance between births and deaths. The relation between L_{inf} and K and is one of four Beverton and Holt invariants identified among life history parameters. The other three relations result from an optimal age at maturity. If age at maturity occurs where Roff's (1992) fecundity function is a maximum, then (Jensen 1996)

(9) $M = 1.50K$

(10) $Mx_{\mathrm{m}} = 1.65$

(11) $L(x_{\mathrm{m}}) = 0.66L_{\mathrm{inf}}$.

Hence, on average, the values of K and x_{m} and the relation between the size of the species L_{inf} and the size at maturity $L(x_{\mathrm{m}})$ are determined by M. For limited taxa, where C_1 is invariant, the relation between size and growth is given by eq. 4. If C_1 is known for a group of species, we can, on average, determine K and x_{m} from M, L_{inf} from K, $L(x_{\mathrm{m}})$ from L_{inf}, W_{inf} from L_{inf} and K, and q from W_{inf} and L_{inf}.

An additional well-known constraint on the life history of an organism is its net reproductive rate or the average number of young produced by an individual during its lifetime. For organisms with indeterminate growth, the reproductive rate R_{o} can be written as

(12) $R_{\mathrm{o}} = l(x_{\mathrm{m}})m0.53W_{\mathrm{inf}}$

where $l(x_{\mathrm{m}})$ is the probability that an individual survives to maturity, $0.53W_{\mathrm{inf}}$ is the average weight of an individual older than age x_{m} with growth described by the von Bertalanffy equation, and m is the number of female young produced per unit weight of adult. At equilibrium

(13) $l(x_{\mathrm{m}})m0.56W_{\mathrm{inf}} = 1$.

Hence, if C_1 is known for a group of species, average values of m, W_{inf}, L_{inf}, q, K, x_{m}, $L(x_{\mathrm{m}})$, and L_{inf} are all determined by M and $l(x_{\mathrm{m}})$, i.e., given the mortality parameters, we can determine many of the remaining life history parameters. These results provide a theoretical basis for estimation of difficult to estimate parameters, such as M and $l(x_{\mathrm{m}})$, using other more easily measured parameters such as the growth parameters.

References

Beverton, R.J.H. 1963. Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **154**: 44–67.

Beverton, R.J.H. 1992. Patterns of reproductive strategy parameters in some marine teleosts fishes. J. Fish Biol. **41**: 137–160.

Beverton, R.J.H., and Holt, S.J. 1959. A review of the lifespans and mortality rates of fish in nature and the relation to growth and other physiological characteristics. *In* Ciba Foundation colloquia in ageing. V. The lifespan of animals. Churchill, London. pp. 142–177.

Charnov, E. 1993. Life history invariants. Oxford University Press, New York.

Charnov, E.L., and Berrigan, D. 1990. Dimensionless numbers and life history evolution: age of maturity versus the adult lifespan. Evol. Ecol. **4**: 273–275.

Cushing, D.H. 1968. Fisheries biology. University of Wisconsin, Madison, Wis.

Holt, S.J. 1962. The application of comparative population studies to fisheries biology — an exploration. *In* The exploitation of natural animal populations. *Edited by* E.D. LeCren and M.W. Holdgate. John Wiley & Sons, New York.

Ivlev, V.S. 1961. The experimental ecology of the feeding of fish. Yale University, New Haven, Conn.

Jensen, A.L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Can. J. Fish. Aquat. Sci. **53**: 820–822.

Pauly, D. 1978. A preliminary compilation of fish length growth parameters. Ber. Inst. Meeresk. Univ. Kiel. **55**: 1–200.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Cons. Int. Explor. Mer, **39**: 175–192.

Roff, D.A. 1992. The evolution of life histories. Chapman and Hall, New York.

Ursin, E. 1967. A mathematical model of some aspects of fish growth, respiration, and mortality. J. Fish. Res. Board Can. **24**: 2355–2390.

Ursin, E. 1979. Principles of growth in fishes. Symp. Zool. Soc. Lond. **44**: 63–87.

Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes

Donald R. Gunderson

Abstract: An interspecific analysis of life history characteristics for 28 stocks of fish showed that age at maturity (α), natural mortality (M), and reproductive effort (gonadosomatic index, GSI) were weakly ($r^2 = 0.18$–0.33) but significantly correlated with body size. Viviparity was associated with reduced reproductive effort, reduced age at maturity, and low M relative to oviparous species of a corresponding size. The allometric relationships of α, M, and GSI with L_∞ showed a high degree of scatter but were in agreement with predictions from models based on metabolic and ecological constraints on assimilation rate. In addition, however, residuals around the GSI–L_∞ and M–L_∞ relationships showed a strong positive correlation ($r^2 = 0.64$), consistent with previous intraspecific manipulation experiments that indicated that reproductive effort and M are genetically linked. A strong positive correlation ($r^2 = 0.75$) was found between GSI and M, and this relationship did not differ significantly between oviparous and viviparous species.

Résumé : Une analyse interspécifiques des caractéristiques du cycle vital de 28 stocks de poisson a révélé que l'âge à maturité (α), la mortalité naturelle (M) et l'effort de reproduction (indice gonadosomatique, IGS) étaient corrélés faiblement ($r^2 = 0{,}18$–$0{,}33$), mais de manière statistiquement significative avec la taille corporelle. La viviparité a été liée à une réduction de l'effort de reproduction, à une réduction de l'âge à maturité et à un faible M comparativement aux espèces ovipares de taille correspondante. Les relations allométriques d'α, de M et de l'IGS avec L_∞ ont montré un degré de dispersion élevé, mais concordaient avec les prévisions établies à l'aide de modèles fondés sur des contraintes métaboliques et écologiques touchant le taux d'assimilation. De plus, les résidus de part et d'autre des relations IGS–L_∞ et M–L_∞ ont montré une corrélation fortement positive ($r^2 = 0{,}64$), concordant avec les expériences de manipulation intraspécifiques antérieures qui indiquaient que l'effort de reproduction et M sont liés au point de vue génétique. Une corrélation fortement positive ($r^2 = 0{,}75$) a été constatée entre l'IGS et M et cette relation n'était pas significativement différente entre les espèces ovipares et vivipares. [Traduit par la Rédaction]

Introduction

Most mathematical models of fish population dynamics include the instantaneous rate of natural mortality (M) as a parameter. These models are used to estimate optimal age at first harvest, stock size, and exploitation rates for commercially fished stocks, so that M usually pertains only to adults. Most studies of fish populations indicate that adult M is independent of fishing mortality (F), relatively constant throughout much of the adult life, and increases sharply once senescence begins (Beverton 1963; Cushing 1975). For most stocks other than prey species (anchovies, herring, etc.) that have been studied, adult M appears to vary little with either age, population size, or time.

Several studies have shown that population dynamics models are quite sensitive to the value chosen for M (Vetter 1988), and a significant amount of effort goes into determining it as accurately as possible. M is a difficult parameter to estimate, typically requiring mark–recapture studies or age determination for large numbers of individual fish. The separation of M from F presents further problems when stocks are under exploitation. Nevertheless, estimates of M for commercially important fishes are probably among the most reliable to be found in the ecological literature due to the importance of accurate values of M in their management.

A number of indirect methods have been developed to estimate M in the absence of the catch-at-age time series or mark–recapture studies usually required. These are based on empirical relationships between M and parameters such as von Bertalanffy growth parameters (L_∞, K; Beverton 1963; Alverson and Carney 1975; Pauly 1980; Charnov 1993; Jensen 1996), reproductive effort (Gunderson 1980; Gunderson and Dygert 1988), and maximum age (Hoenig 1983). Myers and Doyle (1983) and Roff (1984) developed theoretical models based on maximization of the Malthusian parameter (r) or net reproductive rate (R_0) that can be used to estimate M, but these are seldom used in actual practice.

A positive correlation between M and reproductive effort is to be expected simply because some combinations (e.g., high mortality and high reproductive effort) persist better than others (e.g., high mortality and low reproductive effort). However, trade-offs between reproductive effort and adult growth or survival have been reported in a wide range of field studies and manipulation experiments for both plants and animals (Stearns 1992). Several optimal life history models have been developed to explain these trade-offs (Roff 1992; Stearns 1992), and their predictions differ depending on the fitness parameter being maximized (r or R_0) and the parameters included in the model. Adult survival, juvenile survival, and the reproductive effort – age schedule (as well as interannual variability in these parameters) all interact in determining the life history pattern for a given species, and their relative importance is difficult to disentangle.

Received April 15, 1996. Accepted October 7, 1996.
J13415

D.R. Gunderson. School of Fisheries 357980, University of Washington, Seattle, WA 98195, U.S.A.
e-mail: dgun@fish.washington.edu

Another possibility is that the correlation between M and reproductive effort arises as a consequence of similarities in the allometric scaling of these parameters. For example, in across-species plots, whole-body rates such as metabolism, production, and ingestion scale with body weight (W) as $W^{0.75}$, while timing variables such as age at maturity and life span scale as (i.e., are proportional to) $W^{0.25}$ (Charnov 1993). Physiological limitation of individual energy budgets has been suggested as a major determinant of this phenomenon (Weiner 1992), occurring due to bottlenecks in either the rate of resource acquisition (foraging rate, rates of digestion and absorption) or the rate of energy expenditure (heat production, mechanical work, or tissue growth). While there is still some debate over this point (Roff 1992), many authors agree that the upper limit to sustainable energy budgets is set by the digestive tract's capacity to assimilate nutrients and energy from food (Weiner 1992). Fonds et al. (1992) found that maximum daily rates of food consumption scaled as $W^{0.74 \text{ to } 0.80}$ for North Sea plaice and flounder. In any event, allometric scalings in life history parameters definitely exist and must be accounted for in any analysis of these parameters.

A high correlation ($r^2 = 0.81$; Gunderson and Dygert 1988) between reproductive effort, as measured by the gonadosomatic index (GSI), and M was previously observed in a study of 18 oviparous and two viviparous stocks of fish, and one objective of this paper is to use a larger database to explore the underlying causes for the GSI–M relationship. Bioenergetic models are used to examine the significance of physiological constraints and allometric scaling and to account for the influence of body size on the correlation between GSI and M. Residual error around allometric relationships is then examined for evidence of variation due to genetic selection for optimal life history patterns.

A second objective is to examine the influence of viviparity on trade-offs in life history parameters, notably the trade-off between reproductive effort and adult survival. Viviparous species provide a "safe harbor" for their offspring during the gestation period, avoiding the extremely high mortality rates (1–68% per day; Dahlberg 1979; Houde 1989) experienced by pelagic eggs and larvae. Life history theory predicts that rockfish species within the genus *Sebastes* (with 30- to 40-d gestation periods) and dogfish (20- to 23-mo gestation period) should consequently have ages at maturity that differ from their oviparous counterparts (Roff 1992). If the correlation between GSI and M is to be used to provide indirect estimates of M for fisheries managment, there is a possibility that separate relationships should be used for oviparous and viviparous species.

Materials and methods

Reproductive effort was estimated using the annualized GSI (wet ovary weight/somatic weight; Gunderson and Dygert 1988), ovary weight being multiplied by the number of batches spawned per year in the case of northern anchovy (a multiple spawner) and divided by 2 in the case of the dogfish (which give birth every other year). Roff (1992, table 5.3) summarized annual energy budgets for three species of lizards and American plaice, and the ranking of the GSI generally agreed with the ranking of reproductive effort indices based on either the proportion of total annual production (= maintenance + growth + reproduction) or the proportion of the surplus annual production (= growth + reproduction) that is devoted to reproduction. A GSI computed in the same manner as in this paper corresponded roughly to the proportion of the total annual production devoted to reproduction.

The GSI was used to estimate reproductive effort for both the oviparous and viviparous species used in this study. There is apparently no maternal energy contribution other than in the form of yolk by pregnant spiny dogfish, nor do females show elevated metabolic rates per gram when pregnant (Pritchard et al. 1958; Gilbert 1981). Rockfish viviparity also appears to be essentially lecithotrophic, with embryonic nutrition being derived from the energy reserves accrued within the ovary during oogenesis (Wourms 1991; Hopkins et al. 1995).

Studies of Pacific herring (Ware 1985; Gunderson and Dygert 1988), North Sea plaice (Rjinsdorp 1991), and English sole, dogfish, and Pacific cod (Gunderson and Dygert 1988) have shown that the GSI tends to be a conservative property and is affected relatively little by interannual and regional variations in environmental conditions, surplus energy available, or stock abundance. The allocation of reproductive energy between fecundity and egg weight does vary between years for North Sea plaice (Rjinsdorp 1991), but in such a manner that the GSI remains relatively constant. Similar trade-offs between fecundity and egg weight have also been reported between different stocks of Atlantic herring (Bradford and Stephenson 1992; Winters et al. 1993).

Data collection could be carefully controlled for 12 stocks (Table 1). These included English sole (*Pleuronectes vetulus*), Pacific cod (*Gadus macrocephalus*) from stocks in the Bering Sea and Washington – British Columbia, Pacific herring (*Clupea pallasi)*, sablefish (*Anoplopoma fimbria*), spiny dogfish (*Squalus acanthias*), Puget Sound rockfish (*Sebastes emphaeus*), shortbelly rockfish (*Sebastes jordani*), yellowtail rockfish (*Sebastes flavidus*), Pacific ocean perch (*Sebastes alutus*), rougheye rockfish (*Sebastes aleutianus*), and copper rockfish (*Sebastes caurinus*). Ovary weight (O) was measured after the eggs had completed vitellogenesis but before they were hydrated, and studies of egg size distributions and ovarian histology were carried out whenever possible to be certain that development had been completed. Histological examination reveals far more detail (such as the presence of oocytes in the migratory nucleus stage) than gross macroscopic assessments of maturity stage and was sometimes required to be certain that development was complete (McDermott 1994). Somatic body weight (B) was measured with the gonads removed and (whenever possible) with the stomach emptied.

Since the allometric relationships of ovary weight and body weight with length often differ (Table 1), the GSI varied somewhat with length and was referenced to the average size of a mature female in the unexploited stock ($\bar{L}$) using the allometric relationships

$$B = al^b$$

and

$$O = cl^d$$

where l = length. The coefficients a–d (Table 1) were estimated by applying ordinary linear regression analysis to the log-transformed data (Gunderson and Dygert 1988) or through nonlinear regression.

GSI values were obtained from the literature for the remaining 16 stocks (Table 2), including northern sand lance (*Ammodytes dubius*), northern anchovy (*Engraulis mordax*), alewife (*Alosa pseudoharengus*), Atlantic herring (*Clupea harengus*), northern pike (*Esox lucius*), Atlantic cod (*Gadus morhua*) from the North Sea, Gulf of St. Lawrence, and northeast Arctic stocks, haddock (*Melanogrammus aeglefinus*) from the North Sea and Grand Banks stocks, walleye pollock (*Theragra chalcogramma*), American plaice (*Hippoglossoides platessoides*), Pacific halibut (*Hippoglossus stenolepis*), North sea plaice (*Pleuronectes platessa*), North Sea sole (*Solea solea*), and Atlantic mackerel (*Scomber scombrus*). The methods used in calculating GSI for these species depended on the form of available data (Gunderson and Dygert 1988) but were selected for use in this study

Table 1. Coefficients for wet somatic weight–length ($B = al^b$) and wet ovary weight–length ($O = cl^d$) for five oviparous and seven viviparous stocks of fish.

	Coefficients				
	a	*b*	*c*	*d*	*d*–*b*
Oviparous species					
English sole[a]	3.83×10^{-6}	3.13	5.40×10^{-9}	3.94	0.81
Bering Sea cod[b]	4.53×10^{-3}	3.21	2.39×10^{-5}	3.98	0.77
Wash.–B.C. cod[a]	2.25×10^{-5}	2.89	1.63×10^{-7}	3.37	0.48
Pacific herring[a]	2.39×10^{-5}	2.86	1.79×10^{-9}	4.41	1.55
Sablefish[c]	1.26×10^{-6}	3.33	1.80×10^{-11}	4.75	1.42
Viviparous species					
Dogfish[a]	3.96×10^{-6}	3.00	8.88×10^{-8}	3.20	0.20
Puget Sound rockfish[d]	5.88×10^{-5}	2.69	5.87×10^{-7}	3.15	0.46
Shortbelly rockfish[e]	8.15×10^{-3}	3.20	1.38×10^{-2}	2.09	−1.11
Yellowtail rockfish[e]	4.00×10^{-2}	2.86	7.59×10^{-5}	3.92	1.06
Pacific ocean perch[f]	8.22×10^{-3}	3.16	4.79×10^{-8}	5.53	2.37
Rougheye rockfish[g]	5.46×10^{-3}	3.28	3.17×10^{-7}	4.76	1.48
Copper rockfish[h]	5.48×10^{-6}	3.20	1.12×10^{-11}	5.04	1.84

[a] Gunderson and Dygert (1988).

[b] H. Zenger, National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, personal communication.

[c] Kastelle (1991).

[d] A.T. Beckmann, Department of Zoology and Parasitology, Ruhr-Universitat Bochum, ND 05-334, 44801 Bochum, Germany, personal communication.

[e] M.B. Eldridge, National Marine Fisheries Service, Southwest Fisheries Science Center, Tiburon Laboratory, 3150 Paradise Dr., Tiburon, CA 94920, personal communication.

[f] Leaman (1988).

[g] McDermott (1994).

[h] Dygert (1986).

only if they were comparable with the 12 stocks for which data collection and analysis were more carefully controlled.

Reliable estimates of both GSI and *M* were required for the species or stocks used in this paper (Table 2). An estimate of *M* was used only if it was based on direct techniques and the techniques used in obtaining it were appropriate for the stock in question (Ricker 1975; Vetter 1988). A further criterion for selecting *M* for commercially exploited stocks was that the estimate resulted in realistic estimates of population size and reasonable hindcasting of catch histories when used in management. Sex-specific estimates of *M* were generally unavailable, so combined estimates were used in all cases.

Age at maturity (α) was determined for all 28 stocks, due to the importance of this parameter in life history theory (Stearns 1992; Roff 1992; Charnov 1993) and its value in terms of describing life history patterns. α was estimated as the age at 50% maturity for females, except in the case of herring, where sex-specific information was unavailable. The preferred standard for selecting α was that it be as representative as possible of preexploitation conditions, and the earliest reliable estimate was always used.

Allometric scalings for *M*, α, and GSI with size were determined through regression of these parameters against size. Size was scaled using the L_∞ parameter from the von Bertalanfy growth equation (Ricker 1975), since it represents the theoretical maximum size attained and shows a clear relationship to life history theory. The L_∞ parameter has an objective statistical basis and was readily available in the literature. L_∞ estimates were generally derived from data for sexes combined, since sex-specific estimates were often unavailable. American plaice were an exception, as the growth parameters were reported for females only.

A relatively simple model (after Roff 1984; Charnov 1993) was used to predict the allometry between α and body size assuming the following.

(1) Annual surplus production ($\mathrm{d}W/\mathrm{d}T$) is proportional to $AW^{0.75}$, where W = body weight and A is a constant of proportionality.

(2) Weight at age 0 ≈ 0 for fish eggs. The equation

$$\mathrm{d}W/\mathrm{d}T = AW^{0.75}$$

then integrates to

$$0.25A\alpha = (W_\alpha)^{0.25}.$$

(3) Since weight is usually an isometric (cubic) function of length in fishes (Table 1), and length at maturity (L_α) is directly proportional to L_∞ (i.e., $L_\alpha = kL_\infty$; Beverton 1992):

$$\alpha \propto (L_\alpha)^{3(0.25)} \propto (L_\infty)^{3(0.25)} = (L_\infty)^{0.75}.$$

By definition, a fully developed ovary from a fish of length L_∞ will weigh approximately $(\mathrm{GSI})(L_\infty)^3$ g. If all surplus energy goes into reproduction when a fish reaches L_∞, assumption (1) consequently predicts that

$$(\mathrm{GSI})(L_\infty)^3 \propto A(L_\infty)^{3(0.75)} \propto A(L_\infty)^{2.25}$$

or

$$\mathrm{GSI} \propto A(L_\infty)^{-0.75}.$$

M has been shown to scale with $W^{-0.25}$ for organisms ranging in size from bacteria to whales (Peterson and Wroblewski 1984; McGurk 1986). Models based on biomass spectrum theory, bioenergetics, spatial patchiness, and optimal life history theory have all been put forth to explain this relationship (Peterson and Wroblewski 1984; McGurk 1986; Charnov 1993), and the underlying causes are probably complex. Nevertheless, there is little disagreement that *M* scales with $W^{-0.25} \propto (L_\infty)^{-0.75}$, and this must be dealt with statistically in any analysis of life history patterns.

Many investigators use ordinary least squares linear regression of log-transformed variables to estimate the parameters for allometric relationships, on the assumption that the *x*-variable (body size) is usually known with much greater precision than the *y*-variable (Charnov 1993). This approach was also used in this study, arranging all regressions so that most of the error was on the *y*-axis. This was true for both

Table 2. Life history parameters used in this study: M (natural mortality coefficient) and GSI (gonadosomatic index) represent annualized values, L_∞ (theoretical maximum length) is measured in centimetres, and α (maturation age) is measured in years.

					Reference(s)[a]			
	M	GSI	L_∞	α	M	GSI	L_∞	α
Sand lance	1.00	0.47	26.2	3	1	2	3	1
Northern anchovy	0.92	0.65	16.6	1	4	5	6	7
Alewife	0.70	0.30	19.9	3	8	9	10	10
Pacific herring	0.56	0.29	26.3	3	11	11	12	13
Atlantic herring	0.23	0.19	30.0	4	14	15	16	17
Pike	0.33	0.18	81.5	2	18	19	19	19
Pollock	0.25	0.09	58.0	4	20	21	20	20, 21
Bering Sea cod	0.37	0.14	97.0	5	22	11	22	22
Wash.–B.C. cod	0.65	0.16	86.6	3	23	11	24	25
North Sea cod	0.20	0.09	114.8	4	26	27	28	26
St. Lawrence cod	0.19	0.13	91.9	6	29	30	31	32
Northeast Arctic cod	0.20	0.09	130.0	10	33	34	35	36
North Sea haddock	0.20	0.13	52.5	3	37	38	39	38
Grand Banks haddock	0.20	0.10	66.3	6	40	41	42	43
English sole	0.26	0.18	37.2	4	44	11	45	45
American plaice	0.23	0.11	59.4	13	46	47	46	46
Pacific halibut	0.19	0.11	109.6	12	48	49	50	49
North Sea plaice	0.10	0.12	68.5	5	37	51	37	52
North Sea sole	0.10	0.08	32.9	3	53	53	53	53
Atlantic mackerel	0.15	0.09	42.1	2	54	55	56	57
Sablefish	0.10	0.15	71.9	5	58	59	60	60
Puget Sound rockfish	0.44	0.10	15.0	2	61	61	61	61
Shortbelly rockfish	0.26	0.07	29.5	2	62	11	62	62
Yellowtail rockfish	0.14	0.10	48.5	10	63	11	64	64
Copper rockfish	0.13	0.11	50.0	6	65	11	65	66
Pacific ocean perch	0.05	0.04	47.0	11	67	11	68	68
Rougheye rockfish	0.04	0.02	54.7	20	69	11	69	70
Dogfish	0.09	0.04	112.6	23	71	11	72	72

[a] Reference(s): (1) Winters 1983; (2) Scott 1972; (3) Winters 1981; (4) Hanan 1981; Stauffer and Picquelle 1981; Anonymous 1978; (5) Hunter and Leong 1981; Parrish et al. 1986; (6) Spratt 1975; (7) Hunter and Macewicz 1980; (8) Eck and Brown 1985; (9) J.S. Diana, School of Natural Resources, University of Michigan, Ann Arbor, MI 48109, personal communication; (10) O'Gorman and Schneider 1986; (11) see Table 1, this study; (12) R.J. Trumble, International Pacific Halibut Commission, University of Washington, P.O. Box 357951, Seattle, WA 98195, personal communication; (13) Taylor 1964; (14) Cushing and Bridger 1966; (15) Hickling 1940; (16) Beverton and Holt 1959; (17) Cushing 1968; (18) Kipling and Frost 1970; (19) Frost and Kipling 1967; (20) Wakabayashi et al. 1990; (21) Sakuri 1982; (22) Thompson 1994; (23) Fournier 1983; (24) Karp 1982; (25) Westrheim 1977; (26) Daan 1975; (27) Oosthuizen and Daan 1974; Daan 1974; (28) Daan 1974; (29) Paloheimo and Kohler 1968; (30) Buzeta and Waiwood 1982; (31) Minet 1978; (32) Beacham 1983; (33) Gulland 1972; (34) O.S. Kjesbu, Institute of Marine Research, P.O. Box 1870, N-5024 Bergen-Nordnes, Norway, personal communication; (35) Garrod 1977; (36) Rollefsen 1953; (37) Beverton and Holt 1957; (38) Raitt 1933; (39) Jones 1962; (40) Halliday 1971; (41) Hodder 1963; Templeman et al. 1978*b*; (42) Templeman et al. 1978*a*; (43) Templeman et al. 1978*b*; (44) Forrester and Ketchen 1963; (45) Van Cleve and El-Sayed 1969; (46) Pitt 1975; (47) Pitt 1964; (48) IPHC Staff 1960; (49) Schmitt and Skud 1978; (50) Southward 1967; (51) Rjinsdorp 1991; Rjinsdorp et al. 1983; (52) Hefford 1916; (53) DeVeen 1976; (54) Hamre 1980; Anonymous 1984; (55) Institute of Marine Research, P.O. Box 1870, N-5024 Bergen-Nordnes, Norway, personal communication; (56) T. Westgård, Institute of Marine Research, P.O. Box 1870, N-5024 Bergen-Nordnes, Norway, personal communication; (57) Anonymous 1984; Lockwood 1988; (58) Sigler 1995; (59) Kastelle 1991; (60) Norris 1989; (61) A.T. Beckmann, Department of Zoology and Parasitology, Ruhr-Universitat Bochum, ND 05-334, 44801 Bochum, Germany, personal communication; (62) S. Ralston, National Marine Fisheries Service, Southwest Fisheries Science Center, Tiburon Laboratory, 3150 Paradise Dr., Tiburon, CA 94920, personal communication; (63) Tagart 1993; (64) Tagart 1991; (65) Gowan 1983; (66) Richards and Cass 1987; (67) Archibald et al. 1981; (68) Gunderson 1977; (69) Nelson and Quinn 1987; (70) McDermott 1994; (71) Wood et al. 1979; (72) Ketchen 1975.

nonlinear allometric regressions and the linear relationship between GSI and M.

However, some error does exist on the x-axis, so regression parameters were also estimated using functional regression (Kendall and Stuart 1987). Both the x- and y-variables were assumed to have a distinct coefficient of variation (CV), with $\lambda = \mathrm{CV}_y^2 / \mathrm{CV}_x^2$ (Kimura 1992). Since all regressions were arranged so that most of the error was on the y-axis, major axis (MA) functional regression, with equal CVs on the x- and y-axes ($\lambda = 1.0$), is inappropriate. While the relative error on the x- and y-axes can never be known exactly, functional regressions with $\lambda = 4$ (i.e., $\mathrm{CV}_y = 2\mathrm{CV}_x$) were carried out in order to evaluate the sensitivity of parameter estimates to error on the x-axis.

Results

The allometric relationships between α, GSI, M, and L_∞ were all significant ($P < 0.05$) for the 21 stocks of oviparous species when using ordinary regression (Table 3). The α versus L_∞ regression was the only statistically significant allometric relationship for the seven viviparous species, probably owing to

Table 3. Tests for viviparity effect in allometric relationship ($y = aL_\infty^b$) between maturation age (α), gonadosomatic index (GSI), and natural mortality coefficient (M) and theoretical maximum length (L_∞) and in the M–GSI relationship ($M = a\text{GSI} + b$).

							Test for viviparity effect			
	All stocks ($n = 28$)		Viviparous stocks ($n = 7$)		Oviparous stocks ($n = 21$)		Ordinary regression		Functional regression	
							F	P	F	P
ln α vs. ln L_∞							8.49	0.002	8.56	0.002
r^2	0.34		0.77		0.38					
F	13.21		16.74		11.58					
P	0.001		0.009		0.003					
Allometric parameters	a	b	a	b	a	b				
Ordinary regression	0.272	0.724	0.034	1.423	0.347	0.616				
Functional regression	0.121	0.930	0.019	1.575	0.232	0.716				
ln GSI vs. ln L_∞							14.09	<0.001	14.53	<0.001
r^2	0.18		0.23		0.48					
F	5.52		1.49		17.71					
P	0.027		0.276		<0.001					
Allometric parameters	a	b	a	b	a	b				
Ordinary regression	0.842	−0.494	0.385	−0.497	2.029	−0.648				
Functional regression	1.696	−0.672	0.602	−0.615	2.710	−0.721				
ln M vs. ln L_∞							5.93	0.008	6.22	0.007
r^2	0.17		0.51		0.23					
F	5.38		5.16		5.56					
P	0.028		0.072		0.029					
Allometric parameters	a	b	a	b	a	b				
Ordinary regression	1.895	−0.549	5.043	−0.987	2.330	−0.545				
Functional regression	5.430	−0.817	11.564	−1.207	4.474	−0.708				
M vs. GSI							0.15	0.866	0.67	0.521
r^2	0.75		0.35		0.76					
F	79.94		2.69		61.75					
P	<0.001		0.16		<0.001					
Regression parameters	a	b	a	b	a	b				
Ordinary regression	1.640	0.041	2.348	0.003	1.648	0.036				
Functional regression	1.871	0.005	5.702	−0.227	1.868	−0.005				

the small sample size involved. However, tests for the reduction in the error sum of squares (Draper and Smith 1981; D.K. Kimura, National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115-0070, personal communication) achieved by introducing a viviparity effect into regression models for all species combined (Table 3) showed that viviparous species clearly differed from oviparous fish in their allometric relationships between α, GSI, or M and L_∞ ($P = 0.008$ or less). This was true whether an ordinary or functional regression model was used. At any given L_∞, viviparous species usually had a greater α (delayed maturity), lower GSI, and lower M than their oviparous counterparts (Figs. 1 and 2).

The allometric scaling of α, GSI, and M with body size was in general agreement with predictions from models based on metabolic or ecological constraints on assimilation rate. Results (all stocks combined) varied, depending on whether ordinary or functional regression was used (Table 3), but α was proportional to $(L_\infty)^{0.72 \text{ to } 0.93}$ (prediction = $(L_\infty)^{0.75}$), GSI to $(L_\infty)^{-0.49 \text{ to } -0.67}$ (prediction = $(L_\infty)^{-0.75}$), and M to $(L_\infty)^{-0.55 \text{ to } -0.82}$ (prediction = $(L_\infty)^{-0.75}$). However, there was a high degree of scatter around the prediction lines for all three allometric relationships (Figs. 1 and 2). Some of this scatter can be explained by the viviparity effect, but ordinary least squares regression results showed that the correlation between α, GSI, or M and L_∞ was relatively weak ($r^2 = 0.38$, 0.48, and 0.23, respectively) even within oviparous stocks.

There was a high correlation between M and reproductive effort ($r^2 = 0.75$), and the M–GSI relationships for oviparous and viviparous species did not differ statistically ($P = 0.866$ for ordinary regression and 0.521 for functional regression), as would be expected on the basis of an examination of the data (Figs. 1 and 2). The intercept constants for the M–GSI regressions were usually near zero, and the ordinary least squares regression for all stocks combined was redone forcing it through the origin. Eliminating the intercept constant in this manner only reduced r^2 from 0.75 to 0.74, and it was concluded that the resulting regression equation, $M = 1.79\text{GSI}$, should be used when predicting M.

Discussion

It is noteworthy that both M and GSI scaled with size in a similar manner (Table 3). Ordinary and functional regression for oviparous species yielded allometric scaling coefficients of $(L_\infty)^{-0.55}$ and $(L_\infty)^{-0.71}$ for M and $(L_\infty)^{-0.65}$ and $(L_\infty)^{-0.72}$ for GSI. The corresponding estimates for all species combined were $(L_\infty)^{-0.55}$ and $(L_\infty)^{-0.82}$ for M and $(L_\infty)^{-0.49}$ and $(L_\infty)^{-0.67}$ for GSI.

Fig. 1. Allometric relationships (lines) between α, *M*, and GSI versus L_∞ (upper left and right and lower left panels) and the *M* versus GSI relationship (lower right panel) as fitted using ordinary least squares regression (oviparous species, open circles; viviparous species, solid circles).

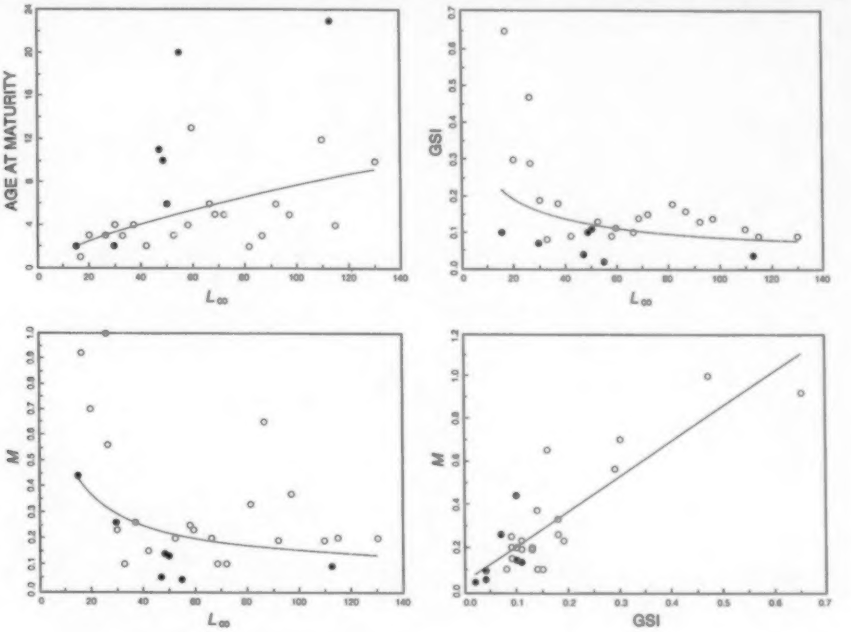
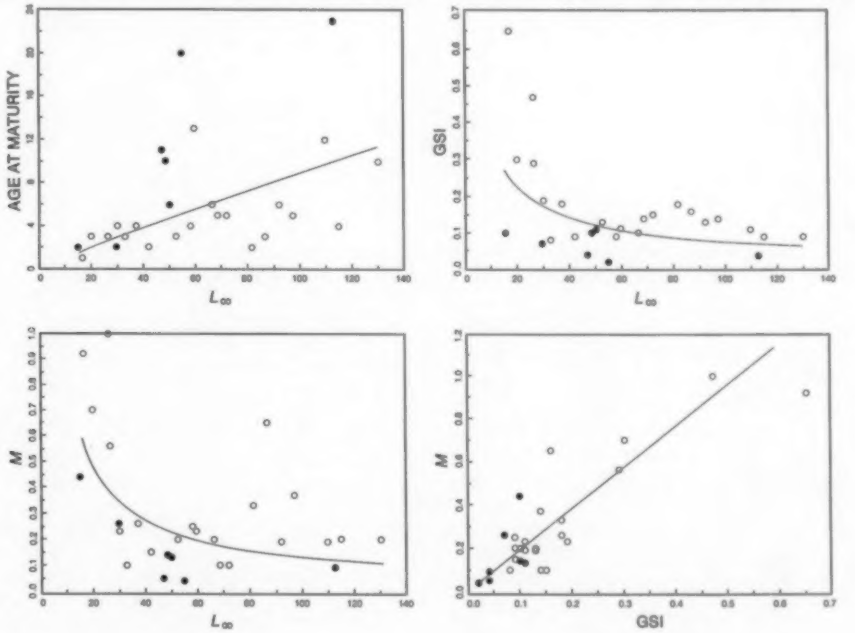
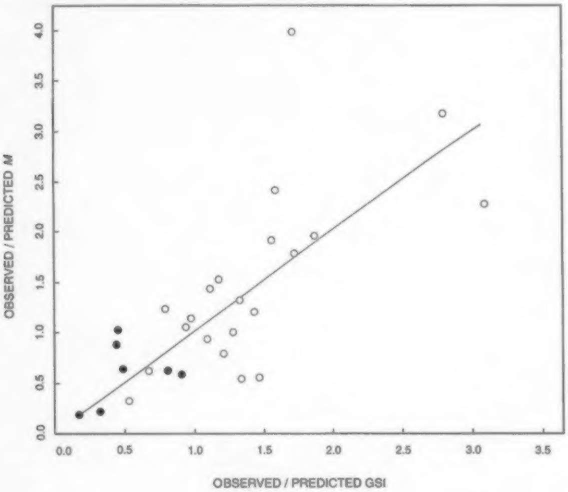


Fig. 2. Allometric relationships (lines) between α, *M*, and GSI versus L_∞ (upper left and right and lower left panels) and the *M* versus GSI relationship (lower right panel) as fitted using functional regression (oviparous species, open circles; viviparous species, solid circles).



Their ratio (*M*/GSI, the slope of the *M*–GSI regression line) is relatively constant from species to species and consequently represents a size-invariant parameter (Charnov 1993). This accounts for the high degree of linearity associated with the *M* versus GSI relationship (Figs. 1 and 2). The relatively high correlation between GSI and *M* results because residuals around the *M* versus L_∞ and GSI versus L_∞ regression lines are positively correlated ($r^2 = 0.64$) so that when the GSI for a

Fig. 3. Residuals from M–L_∞ ordinary regression line versus residuals from the GSI–L_∞ regression line. Points indicate the ratio of observed to predicted values (= exp(ln observed value – ln predicted value)) for oviparous species (open circles) and viviparous (solid circles) species. Observed/predicted ratios for M and GSI are equal along the line indicated.



given species is higher than would be predicted on the basis of its L_∞, so is M (Fig. 3).

Viviparous species clearly follow different life history patterns than oviparous species of a similar size, maturing later in life, putting less energy into reproductive effort, and living longer (Figs. 1 and 2). Since viviparity obviously results in lower egg and larval mortality rates, delayed maturity is expected on the basis of life history theory. Roff (1992) reviewed several different modeling approaches that predict that decreased larval or juvenile mortality rates result in delayed maturation. The models indicated that mortality prior to maturation is far more important than adult mortality in determining optimal age at maturity.

A wide variety of comparative studies across taxa, as well as field studies and manipulation experiments within taxa, have shown that reproductive effort and adult mortality are positively correlated (Roff 1992; Stearns 1992), and the strong correlation between GSI and M observed in this study is in keeping with these. While this analysis compared interspecific differences in life history, the results agree with those from manipulation experiments with field and laboratory populations of guppy (*Poecilia reticulata*). Both increased reproductive effort and earlier maturation have been experimentally induced by increasing adult mortality in field populations (Reznick et al. 1990), and subsequent rearing experiments showed that these changes had a genetic basis.

One explanation, based on bioenergetic constraints, is that the reproductive effort – adult survival trade-off is a secondary result of the trade-off between reproductive effort and growth. If most surplus energy goes into reproduction after sexual maturation, early maturation implies reduced body size. The $(L_\infty)^{-0.75}$ scaling of M and GSI then implies that both adult mortality and reproductive effort will increase as a consequence of early maturation.

However, the high degree of scatter around the M–L_∞ and GSI–L_∞ relationships (Figs. 1 and 2) indicates that simple bioenergetic models can provide only a partial explanation of the high correlation between M and GSI. The residuals around the M–L_∞ relationship show a high positive correlation ($r^2 = 0.64$) with those around the GSI–L_∞ relationship, and the observed/predicted ratios (= exp(ln observed value – ln predicted value)) for M and GSI tend to be similar for any given species (Fig. 3). For example, when the M value observed for a species is twice as high as would be predicted on the basis of its L_∞, its observed GSI value also tends to be twice as high as predicted. There appears to be a definite trade-off between reproductive effort and adult survival even after body size has been adjusted for, and as a consequence the correlation between GSI and M is far higher than that characterizing the underlying allometric relationships.

Acknowledgements

This research was supported in part by grants from the U.S. National Marine Fisheries Service and Washington Sea Grant. Assistance by Dr. Dan Kimura in carrying out functional regression analysis is gratefully acknowledged.

References

Alverson, D.L., and Carney, M.J. 1975. A graphic review of the growth and decay of population cohorts. J. Cons. Cons. Int. Explor. Mer, **36**: 133–143.

Anonymous. 1978. Implementation of northern anchovy fishery management plan. Fed. Register **43**(141): 31 651 – 31 783.

Anonymous. 1984. Report of the mackerel working group. ICES CM 1984/Assess.1.

Archibald, C.P., Shaw, W., and Leaman, B.M. 1981. Growth and mortality estimates of rockfishes (Scorpaenidae) from B.C. coastal waters, 1977–1979. Can. Tech. Rep. Fish. Aquat. Sci. No. 1048.

Beacham, T.D. 1983. Growth and maturity of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can. Tech. Rep. Fish. Aquat. Sci. No. 1142.

Beverton, R.J.H. 1963. Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **154**: 44–67.

Beverton, R.J.H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. J. Fish Biol. **41**(Suppl. B): 137–160.

Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. Fish. Invest. (Ser. 2), **19**.

Beverton, R.J.H., and Holt, S.J. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. CIBA Found. Colloq. Ageing, **5**: 142–177.

Bradford, R.G., and Stephenson, R.L. 1992. Egg weight, fecundity, and gonad weight variability among northwest Atlantic herring (*Clupea harengus*) populations. Can. J. Fish. Aquat. Sci. **49**: 2045–2054.

Buzeta, M.I., and Waiwood, K.G. 1982. Fecundity of Atlantic cod (*Gadus morhua*) in the southwestern Gulf of St. Lawrence. Can. Tech. Rep. Fish. Aquat. Sci. No. 1110.

Charnov, E.L. 1993. Life history invariants: some explorations of symmetry in evolutionary ecology. Oxford University Press, Oxford.

Cushing, D.H. 1968. Fisheries biology: a study in population dynamics. University of Wisconsin Press, Madison, Wis.

Cushing, D.H. 1975. The natural mortality of the plaice. J. Cons. Cons. Int. Explor. Mer, **36**: 150–157.

Cushing, D.H., and Bridger, J.P. 1966. The stock of herring in the

North Sea and changes due to fishing. U.K. Minist. Agric. Fish. Fish. Invest. Ser. 2, **25**(1): 1–123.

Daan, N. 1974. Growth of North Sea cod, *Gadus morhua*. Neth. J. Sea Res. **8**: 27–48.

Daan, N. 1975. Consumption and production in the North Sea cod, *Gadus morhua*: an assessment of the ecological status of the stock. Neth. J. Sea Res. **9**: 24–55.

Dahlberg, M.D. 1979. A review of survival rates of fish eggs and larvae in relation to impact assessments. Mar. Fish. Rev. **41**: 1–12.

DeVeen, J.F. 1976. On changes in some biological parameters in the North Sea sole (*Solea solea* L.). J. Cons. Cons. Int. Explor. Mer, **37**: 60–90.

Draper, N.R., and Smith, H. 1981. Applied regression analysis. 3rd ed. John Wiley & Sons, New York.

Dygert, P.H. 1986. Management implications of variability in reproduction and growth of commercial marine fishes. Ph.D. thesis, University of Washington, Seattle, Wash.

Eck, G.W., and Brown, E.H., Jr. 1985. Lake Michigan's capacity to support lake trout (*Salvelinus namaycush*) and other salmonines: an estimate based on the status of prey populations in the 1970s. Can. J. Fish. Aquat. Sci. **42**: 449–454.

Fonds, M., Cronie, R., Vethaak, A.D., and van der Puyl, P. 1992. Metabolism, food consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature. Neth. J. Sea Res. **29**: 127–143.

Forrester, C.R., and Ketchen, K.S. 1963. A review of the Strait of Georgia trawl fishery. Bull. Fish. Res. Board Can. No. 139.

Fournier, D.A. 1983. An analysis of the Hecate Strait Pacific cod fishery using an age structured model incorporating density-dependent effects. Can. J. Fish. Aquat. Sci. **40**: 1233–1243.

Frost, W.E., and Kipling, C. 1967. A study of reproduction, early life, weight–length relationship and growth of pike, *Esox lucius* L., in Windermere. J. Anim. Ecol. **36**: 651–693.

Garrod, D.J. 1977. The North Atlantic cod. *In* Fish population dynamics. *Edited by* J.A. Gulland. John Wiley & Sons, London, New York, Sydney, Toronto. pp. 216–242.

Gilbert, P.M. 1981. Patterns of shark reproduction. Oceans, **24**(4): 30–39.

Gowan, R.E. 1983. Population dynamics and exploitation rates of rockfish (*Sebastes* sp.) in Central Puget Sound, Washington. Ph.D. thesis, University of Washington, Seattle, Wash.

Gulland, J.A. 1972. Population dynamics of world fisheries. Univ. Wash. Sea Grant Publ. WSG 72-1.

Gunderson, D.R. 1977. Population biology of Pacific ocean perch, *Sebastes alutus*, stocks in the Washington – Queen Charlotte Sound region, and their response to fishing. Fish. Bull. **75**: 369–403.

Gunderson, D.R. 1980. Using *r–K* selection theory to predict natural mortality. Can. J. Fish. Aquat. Sci. **37**: 2266–2271.

Gunderson, D.R., and Dygert, P.H. 1988. Reproductive effort as a predictor of natural mortality rate. J. Cons. Cons. Int. Explor. Mer, **44**: 200–209.

Halliday, R.G. 1971. Recent events in the haddock fishery of the eastern Scotian Shelf. Int. Comm. Northwest Atl. Res. Bull. **8**: 49–58.

Hamre, J. 1980. Biology, exploitation, and management of the Northeast Atlantic mackerel. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **177**: 212–242.

Hanan, D. 1981. Update of the estimated mortality rate of *Engraulis mordax* in southern California. Calif. Fish Game, **61**: 62–65.

Hefford, A.E. 1916. Report on sexual differentiation in the biology and distribution of plaice in the North Sea. U.K. Minist. Agric. Fish. Fish. Invest. Ser. 2, **3**(2): 1–73.

Hickling, C.F. 1940. The fecundity of herring of the southern North Sea. J. Mar. Biol. Assoc. U.K. **24**: 619–632.

Hodder, V.M. 1963. Fecundity of Grand Bank haddock. J. Fish. Res. Board Can. **20**: 1465–1487.

Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. **82**: 898–903.

Hopkins, T.E., Eldridge, M.B., and Cech, J.J., Jr. 1995. Metabolic costs of viviparity in yellowtail rockfish, *Sebastes flavidus*. Environ. Biol. Fishes, **43**: 77–84.

Houde, E.D. 1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish. Bull. **87**: 471–495.

Hunter, J.R., and Leong, R. 1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. Fish. Bull. **79**: 215–230.

Hunter, J.R., and Macewicz, B.J. 1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. **21**: 139–149.

IPHC Staff. 1960. Utilization of Pacific halibut stocks: yield per recruitment. Int. Pac. Halibut Comm. Sci. Rep. No. 28.

Jensen, A.L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Can. J. Fish. Aquat. Sci. **53**: 820–822.

Jones, R. 1962. Haddock bionomics. 2. The growth of haddock in the North Sea and at Faroe. Scotl. Dep. Agric. Fish. Mar. Res. **1962**(2): 1–19.

Karp, W.A. 1982. Biology and management of Pacific cod (*Gadus macrocephalus* Tilesius) in Port Townsend, Washington. Ph.D. thesis, University of Washington, Seattle, Wash.

Kastelle, C.R. 1991. Radioisotope age validation and an estimate of natural mortality from the gonad to somatic weight index for sablefish (*Anoplopoma fimbria*). M.S. thesis, University of Washington, Seattle, Wash.

Kendall, M.G., and Stuart, A. 1987. The advanced theory of statistics. Vol. 2. Classical inference and relationship. 5th ed. Griffin, London.

Ketchen, K.S. 1975. Age and growth of dogfish *Squalus acanthias* in British Columbia waters. J. Fish. Res. Board Can. **32**: 43–59.

Kimura, D.K. 1992. Symmetry and scale dependence in functional relationship regression. Syst. Biol. **4**: 233–241.

Kipling, C., and Frost, W.E. 1970. A study of the mortality, population numbers, year class strengths, production and food consumption of pike, *Esox lucius* L., in Windermere from 1944 to 1962. J. Anim. Ecol. **39**: 115–157.

Leaman, B.M. 1988. Reproductive and population biology of Pacific ocean perch (*Sebastes alutus* (Gilbert)). Ph.D. thesis, University of British Columbia, Vancouver, B.C..

Lockwood, S.J. 1988. The mackerel: its biology, assessment and the management of a fishery. Fishing News Books Ltd., Farnham, Surrey, England.

McDermott, S.F. 1994. Reproductive biology of rougheye and shortraker rockfish, *Sebastes aleutianus* and *Sebastes borealis*. M.S. thesis, University of Washington, Seattle, Wash.

McGurk, M.D. 1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. Mar. Ecol. Prog. Ser. **34**: 227–242.

Minet, J.P. 1978. Dynamics and yield assessment of the northeastern Gulf of St. Lawrence cod stock. Int. Comm. Northwest Atl. Sel. Pap. **3**: 7–16.

Myers, R.A., and Doyle, R.W. 1983. Predicting natural mortality rates and reproduction–mortality trade-offs from life history data. Can. J. Fish. Aquat. Sci. **40**: 612–620.

Nelson, B., and Quinn, T.J., II. 1987. Population parameters for rougheye rockfish (*Sebastes aleutianus*). *In* Proceedings of the International Rockfish Symposium. Alaska Sea Grant Rep. No. 87-2. pp. 209–228.

Norris, J.G. 1989. Comparative analysis of harvesting strategies for sablefish stocks off the coasts of Washington, Oregon and California. Ph.D. thesis, University of Washington, Seattle, Wash.

O'Gorman, R.O., and Schneider, C.P. 1986. Dynamics of alewives in Lake Ontario following a mass mortality. Trans. Am. Fish. Soc. **115**: 1–14.

Oosthuizen, E., and Daan, N. 1974. Egg fecundity and maturity of North Sea cod, *Gadus morhua*. Neth. J. Sea Res. **8**: 378–397.

Paloheimo, J.E., and Kohler, A.C. 1968. Analysis of the Southern Gulf of St. Lawrence cod population. J. Fish. Res. Board Can. **25**: 555–578.

Parrish, R.H, Mallicoate, D.L., and Klingbeil, R.A. 1986. Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis mordax*. Fish. Bull. **84**: 503–517.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Cons. Int. Explor. Mer, **39**: 175–192.

Peterson, I., and Wroblewski, J.S. 1984. Mortality rate of fishes in the pelagic ecosystem. Can. J. Fish. Aquat. Sci. **41**: 1117–1120.

Pitt, T.K. 1964. Fecundity of the American plaice, *Hippoglossoides platessoides* (Fabr.) from Grand Bank and Newfoundland areas. J. Fish. Res. Board Can. **21**: 597–612.

Pitt, T.K. 1975. Changes in abundance and certain biological characteristics of Grand Bank American plaice, *Hippoglossoides platessoides*. J. Fish. Res. Board Can. **32**: 1383–1398.

Pritchard, A.W., Florey, E., and Martin, A.W. 1958. Relationship between metabolic rate and body size in an elasmobranch (*Squalus suckleyi*) and in a teleost (*Ophiodon elongatus*). J. Mar. Res. **17**: 403–411.

Raitt, D.S. 1933. The fecundity of the haddock. Sci. Invest. Fish. Board Scotl. **1932**: 1–42.

Reznick, D.A., Bryga, H., and Endler, J.A. 1990. Experimentally induced life-history evolution in a natural population. Nature (Lond.), **346**: 357–359.

Richards, L.J., and Cass, A.J. 1987. The British Columbia inshore rockfish fishery: stock assessment and fleet dynamics of an unrestricted fishery. *In* Proceedings of the International Rockfish Symposium. Alaska Sea Grant Rep. No. 87-2. pp. 299–308.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

Rijnsdorp, A.D. 1991. Changes in fecundity of female North Sea plaice (*Pleuronectes platessa* L.) between three periods since 1990. ICES J. Mar. Sci. **48**: 253–280.

Rijnsdorp, A.D., van Lent, F., and Groeneveld, K. 1983. Fecundity and the energetics of reproduction and growth of North Sea plaice (*Pleuronectes platessa* L.). ICES C.M. 1983/G:31.

Roff, D.A. 1984. The evolution of life history parameters in teleosts. Can. J. Fish. Aquat. Sci. **41**: 989–1000.

Roff, D.A. 1992. The evolution of life histories: theory and analysis. Chapman and Hall, New York.

Rollefsen, G. 1953. Observations on the cod and cod fisheries of Lofoten. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **136**: 40–47.

Sakuri, Y. 1982. Reproductive ecology of walleye pollock *Theragra chalcogramma* (Pallas). Ph.d. thesis, Hokkaido University, Hakodate, Japan. (Translated from Japanese by T. Nishida, N.D. Davis, and T. Nishiyama, University of Washington, Seattle. 1984)

Schmitt, C.C., and Skud, B.E. 1978. Relation of fecundity to long-term changes in growth, abundance and recruitment. Int. Pac. Halibut Comm. Sci. Rep. No. 66.

Scott, J.S. 1972. Morphological and meristic variation in Northwest Atlantic sand lances (*Ammodytes*). J. Fish. Res. Board Can. **29**: 1673–1678.

Sigler, M.F. 1995. Estimation of survey catchability with an age-structured population model. Sect. 4. Appendix. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska as projected for 1996. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

Southward, G.M. 1967. Growth of Pacific halibut. Int. Pac. Halibut Comm. Rep. No. 43.

Spratt, J.D. 1975. Growth rate of the northern anchovy, *Engraulis mordax*, in Southern California waters, calculated from otoliths. Calif. Fish Game, **31**: 116–126.

Stauffer, G.D., and Picquelle, S.J. 1981. Estimate of the spawning biomass of the northern anchovy central subpopulation for the 1980–81 fishing season. Calif. Coop. Oceanic Fish. Invest. Rep. **22**: 8–13.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, Oxford.

Tagart, J.V. 1991. Population dynamics of yellowtail rockfish (*Sebastes flavidus*) stocks in the northern California to southwest Vancouver Island region. Ph.D. thesis, University of Washington, Seattle, Wash.

Tagart, J.V. 1993. Status of the yellowtail rockfish resource in 1993. Append. E. *In* Appendices to the status of the Pacific Coast groundfish fishery through 1993 and recommended acceptable biological catches for 1994. Pacific Fishery Management Council, 2000 SW First Ave., Suite 420, Portland, OR 97201.

Taylor, F.H.C. 1964. Life history and present status of British Columbia herring stocks. Bull. Fish. Res. Board Can. No. 143.

Templeman, W., Hodder, V.M., and Wells, R. 1978*a*. Age, growth, year-class strength, and mortality of the haddock, *Melanogrammus aeglefinus*, on the southern Grand Bank and their relation to the haddock fishery of this area. Int. Comm. Northwest Atl. Res. Bull. **13**: 31–52.

Templeman, W., Hodder, V.M., and Wells, R. 1978*b*. Sexual maturity and spawning in haddock, *Melanogrammus aeglefinus*, of the southern Grand Bank. Int. Comm. Northwest Atl. Res. Bull. **13**: 53–65.

Thompson, G.G. 1994. Chap. 2. Pacific cod. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands region as projected for 1995. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

Van Cleve, R., and El-Sayed, S.Z. 1969. Age, growth and productivity of an English sole (*Parophrys vetulus*) population in Puget Sound, WA. Bull. Pac. Mar. Fish. Comm. **7**: 51–72.

Vetter, E.F. 1988. Estimation of natural mortality in fish stocks: a review. Fish. Bull. **86**: 25–43.

Wakabayashi, K., Watanabe, K., and Watanabe, Y. 1990. Assessments of walleye pollock abundance of the Southeast Pacific coast of Hokkaido, based on catch statistics and survey data. Int. North Pac. Fish. Comm. Bull. **50**: 101–120.

Ware, D.M. 1985. Life history characteristics, reproductive value, and resilience of Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. **42**(Suppl. 1): 127–137.

Weiner, J. 1992. Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. Trends Ecol. Evol. **7**: 384–388.

Westrheim, S.J. 1977. Length–weight and length–girth relationships, maturity, spawning season and diet of Pacific cod (*Gadus macrocephalus*) collected in British Columbia waters during April 1975 – February 1976. Fish. Res. Board Can. Manuscr. Rep. No. 1420.

Winters, G.H. 1981. Growth patterns in sand lance, *Ammodytes dubius*, from the Grand Bank. Can. J. Fish. Aquat. Sci. **38**: 841–846.

Winters, G.H. 1983. Analysis of the biological and demographic parameters of the northern sand lance, *Ammodytes dubius*, from the Newfoundland Grand Bank. Can. J. Fish. Aquat. Sci. **40**: 409– 419.

Winters, G.H., Wheeler, J.P., and Stansbury, D. 1993. Variability in the reproductive output of spring-spawning herring in the northwest Atlantic. ICES J. Mar. Sci. **50**: 15–25.

Wood, C.C., Ketchen, K.S., and Beamish, R.J. 1979. Population dynamics of spiny dogfish (*Squalus acanthias*) in British Columbia waters. J. Fish. Res. Board Can. **36**: 647–656.

Wourms, J.P. 1991. Reproduction and development of *Sebastes* in the context of the evolution of piscine viviparity. Environ. Biol. Fishes, **30**: 111–126.

Marine zooplanktonic and benthic community respiration rates at Resolute, Canadian high Arctic

Harold E. Welch, Timothy D. Siferd, and Philip Bruecker

Abstract: Benthic community respiration rates and macrozooplankton (>202 μm) biomass and respiration rates were measured throughout a calender year at Resolute (74°42′N, 94°50′W). The plankton averaged 7.2 g dry weight·m^{-2} with no seasonal pattern and respired 82 g O$_2$·m^{-2}·yr^{-1}. Gelatinous and chaetognath predators made up 10% of macrozooplankton biomass and respired 6.4% of planktonic respiration. The lipid content of the nongelatinous fraction fluctuated seasonaly from 64% of dry weight in midwinter to 46% in early summer. The benthic soft-bottom community inside Resolute Bay respired about 125 g O$_2$·m^{-2}·yr^{-1}, with a twofold rate increase in late summer. Offshore on hard bottom the few measurements we obtained suggested a respiration rate of about 75 g O$_2$·m^{-2}·yr^{-1}. The macrozooplankton and benthos were therefore approximately equal in energy flow. The total ecosystem respiration of 157 g O$_2$·m^{-2}·yr^{-1} corroborated a previous independent estimate of photosynthesis of 60 g C·m^{-2}·yr^{-1} for the region. Microplankton respiration appeared to be relatively low. Our results are consistent with the hypothesis that the proporion of primary production exported to the benthos increases with decreasing water temperature and depth, increasing latitude, and increasing cell size.

Résumé : Les taux de respiration de la communauté benthique ainsi que la biomasse et le taux de respiration du macrozooplancton (> 202 μm) ont été mesurés pendant une année civile complète à Resolute (74°42′N, 94°50′W). La biomasse de zooplancton était en moyenne de 7,2 g en poids sec·m^{-2} sans qu'il y ait de motifs saisonniers et le taux de respiration de 82 g O$_2$·m^{-2}·a^{-1}. Les prédateurs gélatineux et chétognates représentaient 10 % de la biomasse de macrozooplancton et leur respiration correspondait à 6,4 % de la respiration planctonique totale. La teneur en lipide de la fraction non gélatineuse a fluctué avec la saison, de 64 % en poids sec au milieu de l'hiver à 46 % au début de l'été. La communauté benthique du fond meuble de la baie Resolute présentait un taux de respiration d'environ 125 g O$_2$·m^{-2}·a^{-1}, taux qui doublait à la fin de l'été. Les quelques mesures que nous avons obtenues au large sur le fond durci indiquent un taux de respiration d'environ 75 g O$_2$·m^{-2}·a^{-1}. Le macrozooplancton et le benthos s'équivalaient presque du point de vue du flux énergétique. La respiration totale de l'écosystème de 157 g O$_2$·m^{-2}·a^{-1} vient corroborer une estimation indépendante antérieure de la photosynthèse qui donnait un résultat de 60 g C·m^{-2}·a^{-1} pour la région. La respiration du microplancton a semblé relativement faible. Nos résultats concordent avec l'hypothèse que la proportion de la production primaire exportée au benthos augmente avec la diminution de la température et de la profondeur de l'eau, avec l'augmentation de la latitude et avec l'augmentation de la taille de la cellule.

[Traduit par la Rédaction]

Introduction

Despite increasing calls for an "ecosystem approach" to environmental problems, whole-ecosystem or whole-community measurements that integrate system properties are rarely reported. One measurement of ecosystem function that is relatively easy to obtain in aquatic systems is respiration. Community and ecosystem respiration rates can be used to estimate total system primary production because the total respiration of an ecosystem is equal to primary production (total photosynthesis), less storage and export. Examples of this approach in the Canadian Arctic are Char Lake (Welch 1974; Welch and Kalff 1974) and the Saqvaqjuac lakes (Welch and Bergmann 1985).

Community respiration can also be used to determine the sources and sinks for energy flow and to compare the structure of similar ecosystems in different regions. In marine systems, the proportion of primary production that is recycled and metabolized by the plankton, relative to the amount exported to the benthic community for respiration and storage, is a complex function of various factors. In general, it appears that the proportion of primary production exported to the benthos increases with decreasing water depth, decreasing water temperature, increasing phytoplankton cell size, and, by extension, increasing latitude (Smetacek 1980; Suess 1980; Forsskall et al. 1982; Davies and Payne 1984; Atkinson and Wacasey 1987; Petersen and Curtis 1980; Carey 1991; Grebmeier and Barry 1991; Wassman 1991). Tight pelagic–benthic coupling at high latitudes is also suggested by stable C and N analysis in the Northeast Water Polynya off northeastern Greenland (Hobson et al. 1995).

While conducting biological oceanographic research on the nearshore marine ecosystem at the Resolute Marine Laboratory

Received December 5, 1995. Accepted October 7, 1996.
J13194

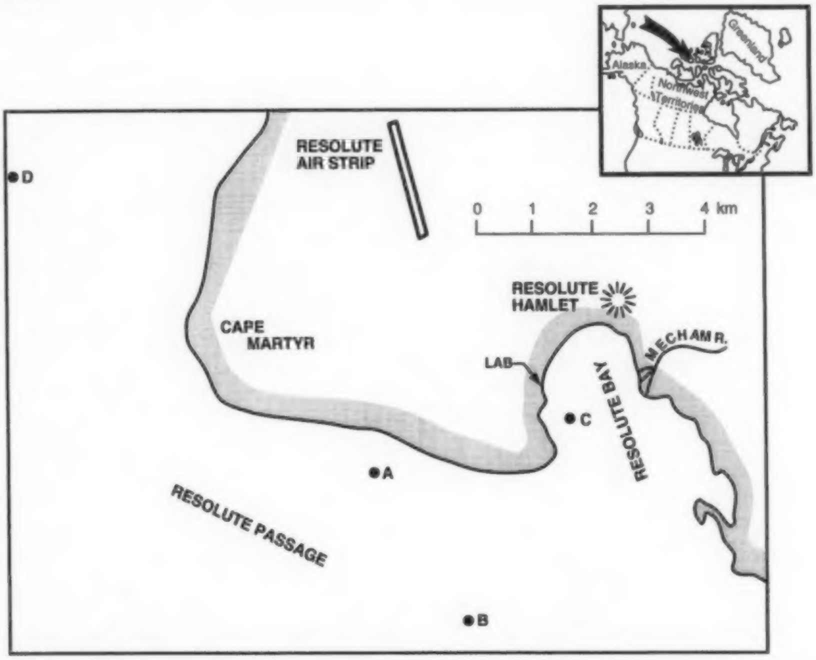
H.E. Welch,[1] T.D. Siferd, and P. Bruecker.[2] Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada.

[1] Author to whom all correspondence should be addressed. e-mail: buster@magic.mb.ca

[2] Present address: 343 E 11th Street, North Vancouver, BC V7L 2H1, Canada.

Can. J. Fish. Aquat. Sci. 54: 999–1005 (1997)

Fig. 1. Map of the Resolute, Northwest Territories, area. A, site of offshore benthic respiration measurements; B, standard oceanographic sampling site, January–October 1993; C, site of Resolute Bay benthic respiration measurements; D, oceanographic sampling site, November–December 1993.



during the 1993 calendar year, we measured the total biomass and respiration rate of the offshore zooplankton community larger than 202 μm and the respiration rate of the benthic community inside and outside Resolute Bay. The objectives were (*i*) to obtain an estimate of annual system respiration to provide an independent estimate of total primary production for comparison with previous estimates of phytoplankton, ice algae, and kelp production (Welch et al. 1992), (*ii*) to determine the relative magnitude of energy flows through the zooplankton and benthic communities to test the hypothesis that export to benthic communities increases with increasing latitude, and (*iii*) to obtain frequent zooplankton biomass values to estimate mean annual abundance and interseasonal fluctuation. We report our results in this paper.

Methods

Description of the study area

Resolute Bay (74°42′N, 94°50′W) (Fig. 1) is well mixed (semidiurnal tidal ranges are 1–2 m). Water currents range from barely detectable beneath the ice in winter to as much as an estimated 0.5 $m \cdot s^{-1}$ during storms in summer. A sill approximately 10 m deep extending across the mouth of the bay limits ice scour to that depth, below which there tends to be accumulation of fine bottom sediments, in part derived from the small Mecham River (87-km^2 watershed; annual discharge 1.52×10^7 m^3) at the head of the bay. The hamlet of Resolute Bay (~180 people) discharges its raw macerated sewage directly into the head of the bay.

Offshore in Resolute Passage, tidal currents are typically 10–25 $cm \cdot s^{-1}$ (Prinsenberg and Bennett 1989; Marsden et al. 1994) and the bottom is composed of silt–clay and small rock overlain by a scoured layer of small limestone cobbles. The bottom at depths <30 m is crisscrossed by ice scours up to 2 m deep. We maintained a standard oceanographic sampling station about 4 km offshore over 108 m water depth from January to June 1993 (site A in Fig. 1). Sampling through the open-water season (late July to late September) occurred in the same area from small boats. In November–December, we sampled at the mouth of Allen Bay over 87 m water depth immediately to the west of Resolute (site B in Fig. 1) because ice in Resolute Passage itself did not consolidate until late December 1993. Water temperatures ranged from −1.8°C in winter up to about −0.5°C in August; salinities were 32–33‰ in winter, with near-surface dilution to 29–32‰ in July–October (see Welch et al. 1996 for annual isopleths).

Zooplankton

Zooplankton were sampled with a vertically hauled nested net, 1.0 m in diameter (0.7854 m^2) by 3 m long. The inner net was 3-mm pore size; the outer net was 202-μm pore size. Each sample was a 100-m vertical tow from bottom to surface hauled at about 0.7 $m \cdot s^{-1}$, replicated four times each sampling day (15–20 min elapsed between samples). The last two sample sets, from Allen Bay, were 85 m vertical distance.

Each sample was emptied and rinsed from the two cod ends into a 4.9-L transparent wide-mouth plastic respiration chamber. Fine screening was then placed over the mouth and held in place with a rubber band, the container submersed and filled with seawater, and the top screwed on underwater to eliminate bubbles. Simultaneous seawater samples were taken for initial dissolved oxygen concentrations. Containers were then placed in covered pails of seawater and held at ambient seawater temperature for 3–4 h, after which the containers were removed, gently shaken, opened, and the oxygen concentration measured with a Radiometer blood-gas Clark-type minielectrode, either by dangling the probe directly into the container or by injecting a filtered water sample into the thermostatted cell holding the probe. The probe was calibrated at least hourly using water analyzed by a slightly modified Winkler oxygen determination

Table 1. Zooplankton dry and carbon weights (±SD) and respiration rates (±SD) at Resolute, 1993.

Date	Nongelatinous zooplankton (g dw·m^{-2})	Gelatinous zooplankton (g dw·m^{-2})	Nongelatinous zooplankton (g C·m^{-2})	Gelatinous zooplankton (g C·m^{-2})	mg O_2·m^{-2}·h^{-1}	mg O_2·g dw^{-1}·h^{-1}	mg O_2·g C^{-1}·h^{-1}
15 Feb.	Σg dw·m^{-2}=15.75±2.07		Σg C·m^{-2}=6.19		27.03±12.70	1.66±0.65	4.37
22 Feb.	Σg dw·m^{-2}=3.32±1.20		Σg C·m^{-2}=1.27		4.20±1.80	1.28±0.34	3.31
2 Mar.	2.69±0.47	2.04±1.10	1.41	0.259	3.19±0.47	0.69±0.12	1.91
12 Mar.	6.46±0.95	2.03±2.19	3.23	0.327	11.32±1.40	1.42±0.34	3.23
20 Mar.	4.31±0.17	1.17±0.76	2.11	0.122	14.56±2.41	2.68±0.39	2.46
26 Mar.	6.65±0.71	3.75±2.18	3.31	0.510	12.64±1.48	1.25±0.21	3.31
3 Apr.	8.78±0.25	6.83±4.03	4.28	0.898	13.40±1.85	0.91±0.29	2.59
12 Apr.	2.82±0.35	3.81±2.07	1.35	0.354	6.47±0.44	1.06±0.32	3.81
21 Apr.	7.51±0.88	0.99±0.25	3.64	0.087	8.95±3.62	1.09±0.52	2.40
8 May	6.46±0.54	1.70±0.84	3.14	0.187	13.71±0.41	1.70±0.18	4.12
17 May	3.47±0.06	1.68±1.39	1.65	0.170	6.80±0.49	1.37±0.27	3.74
4 June	1.83±0.17	1.11±0.87	0.79	0.119	4.44±0.41	1.62±0.48	4.87
16 June	4.04±0.11	1.76±1.08	1.67	0.127	—	—	—
23 June	4.41±0.56	1.70±0.32	1.89	0.170	—	—	—
15 Sept.	2.79±0.52	0.19±0.16	1.27	0.028	4.56±0.60	1.59±0.39	3.51
17 Sept.	5.53±0.68	0.13±0.02	2.43	0.020	3.38±0.47	0.63±0.06	1.38
24 Sept.	2.86±0.49	0.35±0.27	—	—	—	—	—
26 Sept.	4.98±0.89	1.08±0.85	2.41	0.114	8.67±0.33	1.50±0.34	2.43
18 Nov.	4.74±1.29	3.25±1.86	2.40	0.471	8.18±2.76	1.04±0.67	2.85
4 Dec.	6.26±0.83	5.11±1.36	3.20	0.429	7.74±1.15	0.69±0.07	2.09
Mean	4.81±1.92	2.15±1.78	2.36±0.97	0.258±0.223	9.37±5.90	1.31±0.50	3.08±0.94

Note: There were four replicates on each date, except for 21 April and 26 September ($n = 3$) and 17 September respiration only ($n = 3$).

(Carpenter 1965). Typically the oxygen concentration dropped 4–6 mg O_2·L^{-1} over the experimental period. Oxygen consumption by raw seawater blanks filtered through 202-µm mesh was undetectable (<0.001 mg O_2·L^{-1}) over 3-d incubation periods.

After oxygen analysis, gelatinous predators were removed from each sample and transferred to a tared plastic weigh boat. The rest of the plankton was filtered through 202-µm screening and scraped into tared aluminum dishes. Both fractions were dried to constant dry weight (dw) at 60°C.

C and N contents of zooplankton were measured by combustion with oxygen followed by differential thermal conductivity with a Leeman Labs 240XA C:H:N analyzer with better than 1% precision. Lipid content was measured gravimetrically after extraction and evaporation with 2:1 chloroform–methanol (analytical precision about ±0.2%).

Benthic respiration rates

Measurements in Resolute Bay were made at 14–16 m depth about 0.8 km south of the laboratory jetty (Fig. 1) over a blanket of fine sediment underlain by rock rubble. The square respiration chambers were 1.0 × 1.0 × 0.20 m high, opaque acrylic plastic, with a rubber-sealed sampling port, stirring propeller, and 5-cm-diameter rubber-stoppered hole in the top. A rope bridle was attached to the four corners and each chamber lowered from the surface by dive tenders in communication with the diver, who placed the chambers on undisturbed bottom. Each chamber was then plugged and sampled (duplicate 55-mL samples in glass syringes) and the oxygen concentration subsequently determined by Winkler titration (slightly modified from Carpenter 1965). Twenty-four hours later the diver gently stirred each chamber with the propeller, measured the depth of placement into the sediment, then drew duplicate water samples for oxygen analysis. Oxygen consumption calculations took into account the time elapsed and inside volume of the chambers.

To measure the respiration rates of the cobbled offshore bottom in Resolute Passage at 14–16 m depth, 10-cm-thick rubber foam was used as a gasket around the bottom and 40 kg of lead placed on each chamber to seal it around the rocks.

Results and discussion

Zooplankton

The zooplankton biomass ranged from 2 to 16 g dw·m^{-2}, with no apparent seasonal pattern, and averaged 7.22 ± 3.73 g·m^{-2} (calculated from Table 1; $n = 20$). An average of 31% (2.15 g) of the total weight was gelatinous predators, mostly *Mertensia ovum* along with *Beroe cucumis* (Ctenophora), and the hydromedusae *Aeginopsis laurentii* and *Aglantha digitale*. The remaining 69% of the biomass (4.81 g) was composed almost entirely of herbivorous copepods (*Calanus glacialis*, *C. hyperboreus*, *Pseudocalanus minutus*, *Oithona* sp., and others) along with the chaetognath *Parasagitta elegans* and the hyperiid amphipod *Themisto libellula*.

Because the gelatinous predators are about 96% water (Larson 1986) with a salt content of 3.3%, their dry weights are mostly inorganic matter, so organic C content is a better measure of relative biomass than simple dry weight. Total plankton C weights averaged 2.74 g C·m^{-2} (range 0.9–6.2), with gelatinous predators averaging 10% of the total (Table 1), a more realistic assessment of their biomass contribution. The C biomass of gelatinous predators covaried weakly with the nongelatinous fracton ($r^2 = 0.33$; $n = 17$), indicating that gelatinous predator abundance was partially correlated with that of its prey.

For the nongelatinous zooplankton, the mean C:N was 6.9 and underwent a pronounced seasonal cycle, with a minimum about 1 July and a maximum in midwinter (Fig. 2). The C:N paralleled the lipid content, which cycled from about 64%

Fig. 2. C:N ratios for nongelatinous (solid circles) and gelatinous (open circles) macrozooplankton at Resolute in 1993.

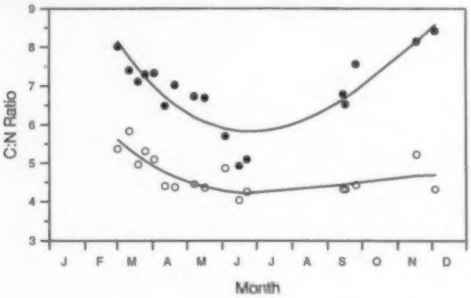
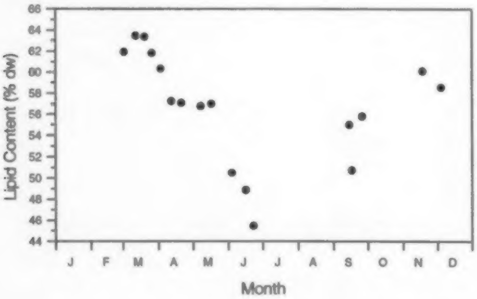


Fig. 3. Lipid content as percentage of dry weight for nongelatinous zooplankton at Resolute in 1993.



maximum in midwinter to 45% minimum in early summer (Fig. 3). The C content of the nongelatinous zooplankton covaried positively with lipid whereas N content covaried negatively (Fig. 4A), resulting in a negative correlation between C and N (Fig. 5). Thus the percentage of C was positively correlated with lipid content, where

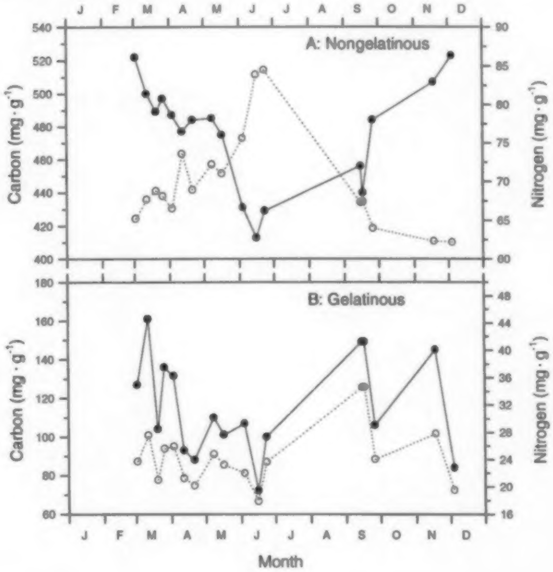
$$(1)\qquad \text{Lipid content} = 4.396(\text{C:N}) + 26.47\ (r = 0.82;\ n = 17).$$

When the lipid stores of nongelatinous zooplankton decreased, the relative percentage of body protein N increased.

The gelatinous predators did not do this. Although their C:N ratio (average 4.7, Fig. 2) also decreased slightly in late winter, C and N covaried positively (Figs. 4B and 5), which we interpret to mean that changes in lipid content accounted for only a small change in body composition, with a trend of decreasing nonlipid body biomass during February–August. This interpretation is consistent with the known low lipid content of the arctic gelatinous predators *M. ovum* (5–14%), *B. cucumis* (4–6%), and *A. digitale* (6–7%) in the eastern Canadian Arctic (Percy and Fife 1981). The decreasing C:N could result from a loss in body weight and higher respiratory losses of C compared with N during the period February–August, when gelatinous predators may be experiencing degrowth.

The total macroplankton respired at an average rate of $9.37\ \text{mg O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ (Table 1) or $82.1\ \text{g O}_2\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. In summer it proved impossible to obtain meaningful bulk zooplankton respiration rates because the samples contained many large diatoms.

Fig. 4. C (solid circles) and N (open circles) contents of (A) nongelatinous zooplankton and (B) gelatinous predators at Resolute in 1993.



We regressed log-transformed oxygen consumption against zooplankton dry weight, where

$$(2)\qquad [\log]\text{mg O}_2\cdot\text{h}^{-1} = 0.376 + 0.737[\log]\text{nongel dw} + 0.0938[\log]\text{gel dw}\ (r = 0.75;\ n = 53).$$

The independent variable [log]nongel dw was significant at $p = 0.0001$. The second variable, [log]gel dw, was marginally significant at $p = 0.032$. At the mean of 4.81 g dw nongelatinous and 2.15 g dw gelatinous zooplankton (Table 1), the gelatinous fraction contributed 7% of total macrozooplankton respiration.

Using C weight:

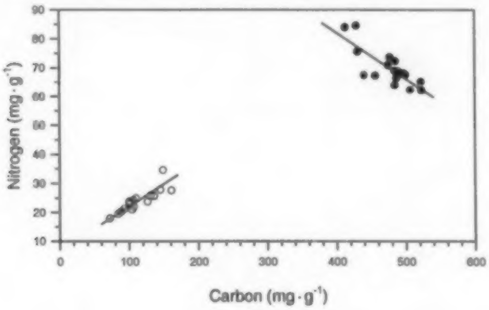
$$(3)\qquad [\log]\text{mg O}_2\cdot\text{h}^{-1} = 0.685 + 0.700[\log]\text{nongel g C} + 0.726[\log]\text{gel g C}\ (r = 0.73;\ n = 53).$$

The independent variable [log]gel g C was nonsignificant ($p = 0.128$). At the mean of 2.36 g nongel C and 0.258 g gel C (Table 1), gelatinous predators accounted for 4.4% of total zooplankton respiration.

In 1993 the predatory chaetognath *P. elegans* constituted an average of 5.7% (0.409 g) of macrozooplankton biomass and respired 1.5% of the total plankton oxygen consumption (Welch et al. 1996). Thus the gelatinous predators (4–5% based on C weight) and chaetognaths together made up about 10% of zooplankton biomass and respired 6.4% of oxygen consumption. The amphipod *T. libellula* was also an important predatory component of the macrozooplankton (unpublished data) and must be added to the chaetognaths and gelatinous predators for an estimate of total predatory zooplankton energy flow.

Our weight-specific zooplankton respiration rates are similar to those determined for individual species by other investigators. For example, Ikeda (1989) measured oxygen consumption for some zooplankters in the Barents Sea in early

Fig. 5. C versus N content of nongelatinous zooplankton (solid circles) and gelatinous predators (open circles) at Resolute in 1993. Regression of N on C for nongelatinous is $Y = -0.160X + 146.2$ ($r^2 = 0.64$) and for gelatinous is $Y = 0.154X + 6.709$ ($r^2 = 0.75$).



summer. The mean respiration rate for adult calanoid copepods between –0.5 and 1.3°C was 0.995 mg $O_2 \cdot g^{-1} \cdot h^{-1}$, compared with our rate of 0.87 mg $O_2 \cdot g^{-1} \cdot h^{-1}$ for a mean of 4.8 g dw nongelatinous zooplankton calculated from equation (1). Ikeda's rate for the hydromedusa *A. digitale* was 0.23 mg $O_2 \cdot g^{-1} \cdot h^{-1}$ at 1.1°C, compared with our calculated rate of 0.19 mg $O_2 \cdot g^{-1} \cdot h^{-1}$ at approximately –1.0°C for gelatinous predators. Percy (1988) reported a mean of 0.12 mg $O_2 \cdot g^{-1} \cdot h^{-1}$ for the ctenophore *M. ovum* in Frobisher Bay, south Baffin Island.

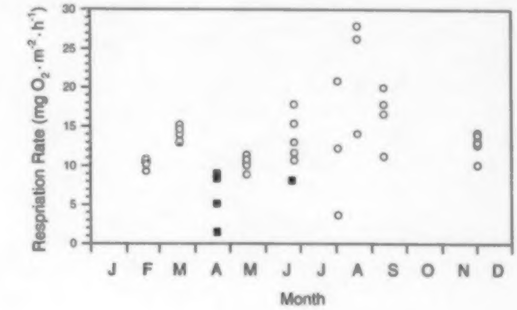
Benthic respiration rates in the bay

Limitations due to dive time, and in summer, an unlucky combination of ice disturbance to mooring lines, and rocks interfering with sealing the chambers, frequently reduced the number of samples below the goal of six per dive. The mean benthic community respiration rate for five "winter" months (February, March, May, June, and December) (Fig. 6) was 12.20 mg $O_2 \cdot m^{-2} \cdot h^{-1}$ ± 1.80 SD, or 79 g $O_2 \cdot m^{-2}$ for 270 "winter" days in Resolute Bay. This is not significantly different from the 13–14 mg $O_2 \cdot m^{-2} \cdot h^{-1}$ reported by Welch and Kalff (1975) for Resolute Bay. The few summer measurements we were able to obtain in the bay resulted in some unrealistically low respiration values. We therefore believe that the higher rates for July–September shown in Fig. 6 are closest to reality. Welch and Kalff (1975) also found that benthic respiration rates in Resolute Bay rose rapidly in August to about 31 mg $O_2 \cdot m^{-2} \cdot h^{-1}$. If we assume an average of 20 mg $O_2 \cdot m^{-2} \cdot h^{-1}$ for July–September, this equals about 46 g $O_2 \cdot m^{-2}$, for a total of 125 g $O_2 \cdot m^{-2} \cdot yr^{-1}$ for the soft-sediment portion of Resolute Bay.

Respiration rates outside the bay

It proved very difficult to obtain respiration rates in the rocky offshore zone because of the uneven bottom. Most measurements showed little or no change in oxygen concentration over 24 h, a sure indication that leakage through the chambers was occurring. Because any leakage reduced the apparent oxygen consumption inside the chambers, we expect that the four highest values we obtained were in fact closest to the actual respiration rate for the offshore benthic community, about 8.5 mg $O_2 \cdot m^{-2} \cdot h^{-1}$ (Fig. 6) or 75 g $O_2 \cdot m^{-2} \cdot yr^{-1}$, about 40% less than the soft-bottom rate inside Resolute Bay.

Fig. 6. Respiration rates for bottom communities in Resolute Bay mud bottom (open circles) and offshore rocky bottom (solid squares). Each point is a single 24-h measurement. February has six observations, March has five, April has five (three in the top block), and December has six.



Total ecosystem respiration rate

Combining the offshore planktonic and Resolute Bay benthic respiration estimates gives 82 (planktonic) + 125 (Resolute Bay benthic) = 207 g $O_2 \cdot m^{-2} \cdot yr^{-1}$. This is probably too high for the bay itself because the shallower water column would have held less plankton than our 100+ m sampling site. A more realistic value can be calculated for the offshore area of Resolute Passage, at 82 (plankton) + 75 for the offshore benthos = 157 g $O_2 \cdot m^{-2} \cdot yr^{-1}$. The benthic and macroplankton communities thus metabolize about equal quantities of the primary production.

Comparison of ecosystem respiration with primary production

Welch et al. (1992) reported primary production to be 54 g $C \cdot m^{-2} \cdot yr^{-1}$ phytoplankton, 5 g $C \cdot m^{-2} \cdot yr^{-1}$ subice algae, and 1 g $C \cdot m^{-2} \cdot yr^{-1}$ kelp, or 60 g $C \cdot m^{-2} \cdot yr^{-1}$ averaged over Barrow Strait. Using an O:C ratio of 2.75, our present estimate of respiration (157 g $O_2 \cdot m^{-2} \cdot yr^{-1}$) is 57.1 g $C \cdot m^{-2} \cdot yr^{-1}$, excluding microplankton respiration, for which we do not have an estimate. There is a strong trophic gradient across Barrow Strait, with annual phytoplankton production near Resolute being about double the average for Barrow Strait (Welch et al. 1992). This, plus the increased importance of local kelp production (an additional source of benthic repiratory C) within Resolute Bay itself, may account for the higher respiration of the sediment community within the bay (125 g O_2 or 45.5 g $C \cdot m^{-2} \cdot yr^{-1}$). Given all the uncertainties, the two independent estimates of total energy flow are remarkably close, strengthening our confidence in the two measurements.

Ecosystem structure and the export of phytoplankton to the benthos

A general understanding of the fate of marine phytoplankton production is emerging. Data and models (Baines et al. 1994) demonstrate that export ratios of phytoplankton production to the benthos increase with increasing production and predict about 40% export at photosynthesis rates of 0.6 g $C \cdot m^{-2} \cdot d^{-1}$, which fits nicely with the Resolute situation, where 54 g $C \cdot m^{-2} \cdot yr^{-1} \div 90\ d = 0.6$ g $C \cdot m^{-2} \cdot d^{-1}$. Planktonic microbial food webs also seem to decrease in relative importance with decreasing water temperature (Pomeroy and Deibel 1986), with relatively high recycling in oligotrophic warm waters dominated by small phytoplankters, for example the Lousiana Shelf in the Gulf of Mexico (Biddanda et al. 1994) and Hawaiian waters (Baines et al. 1994). Andersen and Dyrssen (1989) reported that whereas the planktonic microbial food web utilized 70–80% of primary production in Alaska coastal waters, only 5% of primary production was processed by planktonic microbial activity in more productive Bering Shelf waters dominated by large diatoms, where sinking rates were estimated at 30–60 $m \cdot d^{-1}$. This is similar to Resolute waters, where both ice algae and the short but intense open-water bloom produce large diatoms with water column chlorophyll concentrations averaging 3–6 $mg \cdot m^{-3}$ in August (Welch et al. 1992 and unpublished data). Simultaneous work on microplankton dynamics at Resolute in 1993 suggested that microplankton respiration was a small percentage of total plankton respiration (R. Rivkin, Memorial University, St John's, Nfld., personal communication).

Petersen and Curtis (1980) compared scanty biomass data for Disko Bugt in south Greenland, the North Sea, and Phanganga Bay in Thailand and concluded that the relative proportion of primary production reaching the benthos versus the zooplankton increased with increasing latitude, being about 1:1 in Disko Bugt (68°N). Our measurements show that at 75°N, the ratio of benthic to planktonic energy flow is also approximately 1:1.

The high proportion of primary production used by the benthos at Resolute probably reflects the relatively rapid sedimentation rate of the summer diatom bloom, assisted by the bivalve *Mya truncata*, which is estimated to filter the upper 15 m of water every 2–3 wk in summer (Welch et al. 1992). Recycling of phytoplankton by the zooplankton also appears to be relatively low. Our data show no increase in weight-specific zooplankton respiration in summer, although small changes would be undetectable because of the high variance (Table 1). Since the average of 54 g C photosynthesis is fixed in July–September, our mean zooplankton respiration rate would account for only 13% of this primary production over that 90-d period. However, the relative constancy of zooplankton energy flow throughout the year must mean that something on the order of 50% of the phytoplankton production is retained in the water column, some of it as lipid storage, for subsequent oxidation during winter and spring.

Our results for Resolute Passage probably cannot be applied directly to the deeper waters of Lancaster Sound to the east. Although rates of primary production are comparable (Welch et al. 1992), the deeper water column holds more zooplankton per unit area (Sameoto 1984). Combined with a longer particle settling time and thus increased opportunity for recycling within microbial food webs, we expect that in Lancaster Sound, and by extension north Baffin Bay, the plankton community accounts for a higher percentage of ecosystem respiration, relative to the 50:50 split between plankton and benthos in Resolute Passage (see also the discussion in Grebmeier and Barry 1991).

We conclude from these results and discussion that the proportion of phytoplankton production exported to the benthos increases with decreasing water temperature and depth and increasing cell size. At high north latitudes under seasonal ice cover the benthos respires 50% or more of primary production in nearshore waters <20 m depth, the percentage decreasing as water depth increases.

Acknowledgements

We thank R. Conover, I. Davies, M. Paterson, and two anonymous referees for reviewing the manuscript. P. Amarualik and H. Landry assisted with the field work. The Polar Continental Shelf Project provided partial logistical support.

References

Andersen, L., and Dyrssen, D. 1989. Chemical oceanography of the Arctic Ocean. *In* The Arctic seas: climatology, oceanography, geology, and biology. *Edited by* Y. Herman. Van Nostrand Reinhold, New York. pp. 93–114.

Atkinson, E.G., and Wacasey, J.W. 1987. Sedimentation in Arctic Canada: particulate organic carbon flux to a shallow marine benthic community in Frobisher Bay. Polar Biol. **8**: 3–7.

Baines, S.B., Pace, M.L., and Karl, D.M. 1994. Why does the relationship between sinking flux and planktonic primary production differ between lakes and oceans? Limnol. Oceangr. **39**: 213–226.

Biddanda, B., Opsahl, S., and Benner, R. 1994. Plankton respiration and carbon flux through bacterioplankton on the Louisiana Shelf. Limnol. Oceanogr. **39**: 1259–1275.

Carey, A.G., Jr. 1991. Ecology of North Amercian Arctic continental shelf benthos: a review. Continental Shelf Res. **11**: 865–883.

Carpenter, J.H. 1965. The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method. Limnol. Oceanogr. **10**: 141–143.

Davies, J.M., and Payne, P. 1984. Supply of organic matter to the sediment in the North Sea during a spring phytoplankton bloom. Mar. Biol. **78**: 315–324.

Forsskall, M.A., Lakkonen, A., and Leppanen, J.M. 1982. Seasonal cycle of production and sedimentation of organic matter at the entrance to the Gulf of Finland. Neth. J. Sea Res. **16**: 290–299.

Grebmeier, J.M., and Barry, J.P. 1991. The influence of oceanographic processes on pelagic–benthic coupling in polar regions: a benthic perspective. J. Mar. Syst. **2**: 495–518.

Hobson, K.A., Ambrose, W.G., Jr., and Renaud, P.E. 1995. Sources of primary production, benthic–pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar. Ecol. Prog. Ser. **128**: 1–10.

Ikeda, T. 1989. Metabolism and elemental composition of zooplankton from the Barents Sea during early arctic summer. Mar. Biol. **100**: 173–183.

Larson, R.J. 1986. Water content, organic content, and carbon and nitrogen composition of medusae from the northeast Pacific. J. Exp. Mar. Biol. Ecol. **99**: 107–120.

Marsden, R.F., Paquet, R., and Ingram, R.G. 1994. Currents under land-fast ice in the Canadian Arctic Archipelago. Part 1: Vertical velocities. J. Mar. Res. **52**: 1017–1036.

Percy, J.A. 1988. Influence of season, size, and temperature on the metabolism of an arctic cydippid ctenophore, *Mertensia ovum* (Fabricius). Sarsia, **73**: 61–70.

Percy, J.A., and Fife, F.J. 1981. The biochemical composition and energy content of arctic marine zooplankton. Arctic, **34**: 307–313.

Petersen, G.H., and Curtis, M.A. 1980. Differences in energy flow through major components of subarctic, temperate and tropical marine shelf ecosystems. Dana, **1**: 53–64.

Pomeroy, L.R., and Deibel, D. 1986. Temperature regulation of bacterial activity during the spring bloom in Newfoundland coastal waters. Science (Washington, D.C.), **233**: 359–361.

Prinsenberg, S.J., and Bennett, E.B. 1989. Transport between Peel Sound and Barrow Strait in the Canadian Arctic. Continental Shelf Res. **9**: 427–444.

Sameoto, D.D. 1984. Vertical distribution of zooplankton biomass and species in northeastern Baffin Bay related to temperature and salinity. Polar Biol. **2**: 213–224.

Smetacek, V. 1980. Annual cycle of sedimentation in relation to plankton ecology in western Kiel Bight. Ophelia (Suppl.), **1**: 65–76.

Suess, E. 1980. Particulate organic flux in the ocean-surface productivity and oxygen utilization. Nature (Lond.), **288**: 260–263.

Wassman, P. 1991. Dynamics of primary production and sedimentation in shallow fiords and polls of western Norway. Oceanogr. Mar. Biol. Annu. Rev. **29**: 87–154.

Welch, H.E. 1974. Metabolic rates of arctic lakes. Limnol. Oceanogr. **19**: 65–73.

Welch, H.E., and Bergmann, M.A. 1985. Winter respiration of lakes at Saqvaqjuac, northern Hudson Bay. Can. J. Fish. Aquat. Sci. **42**: 494–505.

Welch, H.E., and Kalff, J. 1974. Benthic photosynthesis and respiration in Char Lake. J. Fish. Res. Board Can. **31**: 609–620.

Welch, H.E., and Kalff, J. 1975. Marine metabolism at Resolute Bay, Northwest Territories. Circumpolar Conference on Northern Ecology. *II*. National Research Council of Canada, Ottawa, Ont. pp. 69–75.

Welch, H.E., Bergmann, M.A., Siferd, T.D., Martin, K.A., Curtis, M.F., Crawford, R.E., Conover, R.J., and Hop, H. 1992. Energy flow through the marine ecosystem of the Lancaster Sound Region, arctic Canada. Arctic, **45**: 343–357.

Welch, H.E., Siferd, T.D., and Bruecker, P. 1996. Population, growth, and respiration of the chaetognath *Parasagitta elegans* in the Canadian high Arctic. Can. J. Fish. Aquat. Sci. **53**: 520–527.

Within-population variability in egg characteristics of walleye (*Stizostedion vitreum*) and white sucker (*Catostomus commersoni*)

Thomas A. Johnston

Abstract: I examined variation in egg characteristics among individual females of sympatrically spawning walleye (*Stizostedion vitreum*) and white sucker (*Catostomus commersoni*) from Lake Manitoba. White sucker produced eggs of greater dry mass and energy content than walleye. Walleye egg dry mass varied between years and was positively related to both female length and age. The relationship between white sucker egg dry mass and female length varied between years. Egg energy density did not vary with respect to female length in either species. Egg energy density varied between years for walleye but not white sucker. Hatching success of walleye eggs was positively related to female age and negatively related to female length adjusted for age. Length and dry mass of walleye larvae at hatch increased with egg dry mass. Results suggest that the quality of eggs produced by walleye and white sucker populations may vary with the size and age structure of the populations and among spawning years.

Résumé : J'ai examiné la variation dans les caractéristiques des oeufs parmi des femelles individuelles de doré jaune (*Stizostedion vitreum*) et de meunier noir (*Catostomus commersoni*) qui frayent sympatriquement dans le lac Manitoba. Le meunier noir a produit des oeufs dont la masse sèche et la teneur en énergie étaient plus élevées que celles du doré jaune. La masse sèche des oeufs de doré jaune a varié d'une année à l'autre et présentait une corrélation positive avec la longueur et l'âge de la femelle. La relation entre la masse sèche des oeufs de meunier noir et la longueur de la femelle présentait une variation annuelle. La densité d'énergie des oeufs ne varie pas avec la longueur de la femelle dans ni l'une ni l'autre des espèces étudiées. La densité d'énergie des oeufs a présenté une variation annuelle chez le doré jaune, mais non chez le meunier noir. Le taux de succès de l'éclosion des oeufs de doré jaune était corrélé positivement avec l'âge de la femelle et négativement avec la longueur de la femelle ajustée selon l'âge. La longueur et la masse sèche des larves de doré jaune à l'éclosion ont augmenté avec la masse sèche des oeufs. Les résultats indiquent que la qualité des oeufs produits par les populations de doré jaune et de meunier noir peut varier avec la structure de taille et d'âge des populations et avec les années. [Traduit par la Rédaction]

Introduction

Walleye (*Stizostedion vitreum*) and white sucker (*Catostomus commersoni*) occur sympatrically over much of their natural ranges and share similar spawning seasons and habitats (Scott and Crossman 1973). Populations of both species show wide interannual variation in the production of larvae (Johnston et al. 1995). Some of this variation may be due to variation in the quantity and quality of eggs spawned, which in turn may be influenced by the size and age structure of the spawning population. Understanding how the reproductive characteristics of a population vary with respect to size and age structure is essential for effective fisheries management (Colby and Nepszy 1981). Increasing fecundity with increasing female size and (or) age has been well documented for both species (Wolfert 1969; Scott and Crossman 1973; Forney 1976; Serns 1982; Munkittrick and Dixon 1988). However, less is known about the influence of female size and age on egg quality in these species.

Egg quality is reflected in the size and composition of the egg. Both may influence the probability of fertilization and the viability of the embryo and larva. Numerous marine and freshwater species show large variation in egg size (reviewed by Bagenal 1971). Both egg size and composition vary with female size and (or) age in a variety of fish species (reviewed by Nikolskii 1969; Kamler 1992; see Discussion). Walleye egg diameter can range from 1.37 to 2.12 mm (Colby et al. 1979) and was positively related to female length in one population (Craig et al. 1995) but not in several others (Wolfert 1969; Serns 1982; Craig et al. 1995). Similarly, no relationship was observed between egg diameter and female length of white sucker (Fuiman and Trojnar 1980). Egg diameter is considered a less accurate indicator of egg quality than dry mass or energy content (Kamler 1992), but neither dry masses nor energy densities have been determined for walleye eggs from individual females. Similarly, few studies have examined dry masses or energy densities of eggs from individual white sucker (Trippel and Harvey 1987). Yolk and oil volumes and fatty acid profiles of walleye eggs vary with egg size, but it is unknown if this variation reflects differences among females in the spawning population (Moodie et al. 1989). In addition, few studies have compared walleye or white sucker egg survival between females of different sizes or ages (Auer and Auer 1987).

Received January 30, 1996. Accepted October 7, 1996.
J13278

T.A. Johnston.[1] Department of Fisheries and Oceans, Gulf Region, Gulf Fisheries Centre, P.O. Box 5030, Moncton, NB E1C 9B6, Canada.

[1] Present address: Department of Fisheries and Oceans, Central and Arctic Region, Freshwater Institute, 501 University Cr., Winnipeg, MB R3T 2N6, Canada.
e-mail: johnstont@dfo-mpo.gc.ca

I believe that intrapopulation variation in egg quality of walleye and white sucker should be examined further. Earlier studies may have failed to find a relationship between egg size and female size because the eggs were sampled before they had fully matured (e.g., Craig et al. 1995) or the egg size was measured as diameter rather than dry mass. In addition, little is known of the variability in energy density or hatchability of these species' eggs with respect to characteristics of the female. This research had two objectives: (1) to assess and compare the within-population variability in egg dry mass and energy density with respect to the size and age of female walleye and white sucker and (2) to examine the effects of female and egg characteristics on egg survival during incubation.

Materials and methods

Mature female walleye and white sucker from Lake Manitoba were captured in pound nets as they ascended Swan Creek during annual spawn-taking operations at the Manitoba Department of Natural Resources' Swan Creek hatchery near Lundar, Manitoba, in April and May of 1994, 1995, and 1996. All fish were in nonspawning condition (eggs not free-flowing) when captured. Captured female walleye were placed in holding nets for several days until they attained spawning condition (eggs free-flowing) before their eggs were stripped. Walleye egg samples were collected on 2 May ($n = 20$ fish) and 6 May ($n = 20$ fish) in 1994, on 5 May ($n = 25$ fish) and 6 May ($n = 15$ fish) in 1995, and on 10 May ($n = 29$ fish) and 14 May ($n = 11$ fish) in 1996. Females were sampled randomly, except with respect to body size. I purposely oversampled the largest and smallest fish in order to obtain a more even female size distribution. A sample (~25 mL in 1994 and 1996 and ~75 mL in 1995) of eggs was collected in a plastic container from the posterior third of the expelled egg volume (i.e., first third expelled) as each fish was stripped. In 1995 only, ~15 mL of these eggs were removed and fertilized for 28 females (see below). The remaining egg sample from these females and all eggs from other females were placed in plastic bags on crushed ice and transported back to the laboratory. Each fish was measured (fork length (FL), ± 10 mm) and the second and third dorsal spines were removed (except in 1994) before being released. White sucker egg samples were collected on 30 April ($n = 26$ fish) and 6 May ($n = 13$ fish) in 1994 and on 6 May ($n = 35$ fish) in 1996. As with walleye, I oversampled the largest and smallest females in order to obtain a more even size distribution. Selected females were killed, packed on ice, and transported back to the laboratory. Each fish was measured (FL, ± 1 mm), a sample of eggs (~25 mL) was dissected from the posterior third of the left ovary, and the first three pectoral fin rays were removed (except in 1994).

Dry mass and ash content of eggs were estimated as follows. I rinsed ~15 mL of eggs from each female of both species by adding ~25 mL of Swan Creek water and swirling them gently for ~30 s. Because the white sucker were not yet in spawning condition, most of the eggs were still loosely held together by connective tissue and blood vessels. Therefore, I selected eggs that separated easily from the others and had no connective tissue or blood vessels attached, as I assumed these to be in the closest condition to those that would have been spawned. Three subsamples (five eggs each for walleye and three eggs each for white sucker) were removed from the samples using forceps. The subsamples were placed on preashed, preweighed aluminum pans (~1.3 mg), dried for 24 h at 60°C, placed in a desiccator for 1 h, and then weighed (± 1 μg) on a Perkin-Elmer AD-6 autobalance (1994) or a Cahn C-33 microbalance (1995 and 1996). Ash contents were determined (except in 1996) by combusting the subsamples for 16 h at 500°C and then reweighing. Approximately 15 mL of the remaining fresh eggs from each sample were dried for 24 h at 60°C and stored at −18°C for energetic determinations.

Energy densities (joules per milligram) of eggs were determined by burning subsamples (6–13 mg dry mass) in a Phillipson microbomb calorimeter (Gentry Instruments, Inc., Aiken, S.C.) following standard calorimetry techniques (Prus 1975). I estimated energy densities of the eggs of 10 fish for each species and year. The 10 fish were selected to cover the entire size range sampled for that species in a given year. Two determinations were made for each fish. Mean egg energy contents (joules per egg) were estimated for each fish as the product of mean egg dry mass and mean egg energy density.

Ages of the fish collected in 1995 and 1996 were determined by counting annuli on walleye dorsal spine sections and white sucker pectoral fin ray sections using a modification of the methods outlined by Chilton and Beamish (1982). Ageing structures were allowed to air dry, set in epoxy, and then sectioned with a Buehler Isomet low-speed saw. Three sections from each fish were mounted in clear epoxy on a glass microscope slide. Sections were viewed under a compound microscope with a dark field condenser at 100× magnification.

I examined hatching success and larval size at hatch using eggs from 28 of the 40 female walleyes sampled in 1995. All eggs were fertilized using semen pooled from three ripe males captured at Falcon Lake, Manitoba, on 1 May 1995. The use of a pooled sperm source for fertilization required the assumption that egg batches of individual females did not differ in the proportions of eggs fertilized by each male. The semen was gently stirred, mixed with an extender (two parts extender to one part semen), as described in Moore (1987), placed in tissue culture flasks to a depth of <2 mm, and then stored in a refrigerator over crushed ice until required. The semen was transported in a cooler with crushed ice to the egg collection site at Swan Creek on 5 and 6 May for fertilization. Eggs from each of the 28 females were fertilized and water hardened separately in the field. A 15-mL subsample of eggs was fertilized with 0.50 mL of the semen–extender mixture and gently stirred with a feather for 2 min. Approximately 100 mL of Swan Creek water was slowly added and the eggs were stirred continuously for another 2 min. The fertilized eggs were stirred in a 400 mg tannic acid·L^{-1} solution for 2 min to reduce adhesion (Waltemyer 1976), rinsed twice, and then placed with ~200 mL of Swan Creek water in 250-mL plastic jars and allowed to harden. Egg jars were placed in a cooler partially filled with water to maintain the eggs at ambient water temperature (7–9°C) during field operations and transport back to the laboratory. In the laboratory, the egg jars were placed in successively warmer water baths over 3 h to raise the incubation temperature to 12°C. Eggs were immersed for 10 min in a 0.7% prepodyne solution (contains 1% titratable iodine, West Chemical Products, Ville D'Anjou, Que.) to inhibit fungal growth and then transferred to the incubation system.

I incubated the walleye eggs in small batches using a flow-through system. Six 70-L stainless steel tubs were immersed in a temperature-controlled water bath. Each tub received a constant inflow of fresh water at a replacement rate of 50% every 12 h and had its own circulation system independent of the other tubs and the water bath. Incubation chambers were plastic tubes (35 mm in diameter, 85 mm long) with 1-mm^2 stainless steel mesh glued to one end. Twenty-eight incubation tubes were placed in each stainless steel tub. The incubation tubes were seated vertically (mesh-end down) into a pipe connecting all 28 tubes. Water was recirculated continuously from the stainless steel tub through the connecting pipe by a small submersible pump such that water flowed up from the bottom and out through the top of the incubation tubes. A 500-μm Nitex screen was inserted at the top of each incubation tube to prevent loss of eggs. I treated each stainless steel tub as a block and randomly assigned the fertilized eggs of the 28 females to the 28 incubation tubes in each of the blocks. Thirty eggs were scattered randomly over the mesh at the bottom of each incubation tube. Water temperature was maintained at 12°C (± 0.5°C) throughout the incubation period. This temperature is in the middle of the optimum range for walleye egg incubation (Koenst and Smith 1976). The laboratory was subjected to a 16 h light : 8 h dark regime.

Mortalities were removed with a pipette and recorded daily from

Table 1. Dry masses, energy densities, and energy contents of eggs sampled from walleye and white sucker of Lake Manitoba during spring 1994, 1995, and 1996.

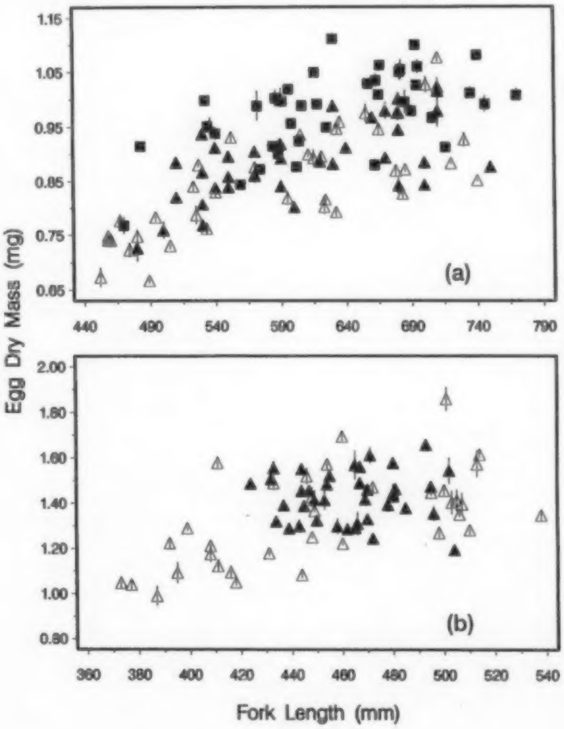
Species	Year	Dry mass (mg·egg^{-1})	Energy density (J·mg dry^{-1})	Energy content (J·egg^{-1})
Walleye	1994	0.894±0.074	25.3±0.89	22.6±1.6
	1995	0.979±0.073	26.6±1.3	25.6±2.6
	1996	0.852±0.096	27.9±0.79	24.4±2.8
White Sucker	1994	1.43±0.11	25.3±0.90	34.8±2.6
	1996	1.33±0.21	24.7±0.55	33.9±5.2

Note: Values represent unadjusted means ± 1 SD. Estimates are based on sample sizes of $n = 40$ fish for walleye egg dry mass in all years, $n = 39$ and $n = 35$ fish for white sucker egg dry mass in 1994 and 1996, respectively, and $n = 10$ fish for energy density and energy content.

day 4 onward. Hatching success was estimated as the percentage of incubated eggs that survived from fertilization to hatch and produced larvae that had straight spines and swam in a straight line. Eggs that produced larvae with deformed spines and erratic swimming behaviour were counted as mortalities. The mesh on the bottom of the incubation tubes was sufficiently small to prevent passage of eggs but large enough to allow some larvae to escape and move freely through the system into other incubation tubes. To avoid the possibility of confusing the larvae of different females with each other, up to 50 of each female's eggs surviving after day 16 were transferred into glass petri dishes filled with water. These eggs were incubated to hatching in a controlled-temperature (12 ± 0.1°C) room with light conditions identical to those of the flow-through system. Water in the petri dishes was replaced once daily. Individual larvae were killed in MS 222 (ethyl *m*-aminobenzoate methanesulfonate) within 24 h of hatching. Total length (± 0.2 mm) was measured using a dissecting scope and ocular micrometer. Larvae were placed on preweighed aluminum pans (~1.3 mg), dried for 24 h at 60°C, placed in a desiccator for 1 h, and then weighed (± 1 μg) on a Cahn C–33 microbalance. Up to 10 larvae from each female were measured.

I analyzed the variation in egg dry mass, energy density, energy content, and hatching success using standard parametric methods (GLM and TTEST procedures, SAS Institute Inc. 1985). Dry mass estimates were $\log_e$-transformed where necessary and hatching success estimates were arcsine-transformed to meet the assumptions of parametric analyses. Female fork length and age were $\log_e$-transformed where necessary to linearize the observed relationships. All tests of significance for analyses of variance (ANOVA) and covariance (ANCOVA) were based on the partial (Type III) sums of squares.

Fig. 1. Scatter plots of egg dry mass versus fork length for (*a*) walleye and (*b*) white sucker females ascending Swan Creek from Lake Manitoba in 1994 (solid triangles), 1995 (solid squares), and 1996 (open triangles). Symbols represent means ± 1 SE. Note the differences in scales of axes between plots.

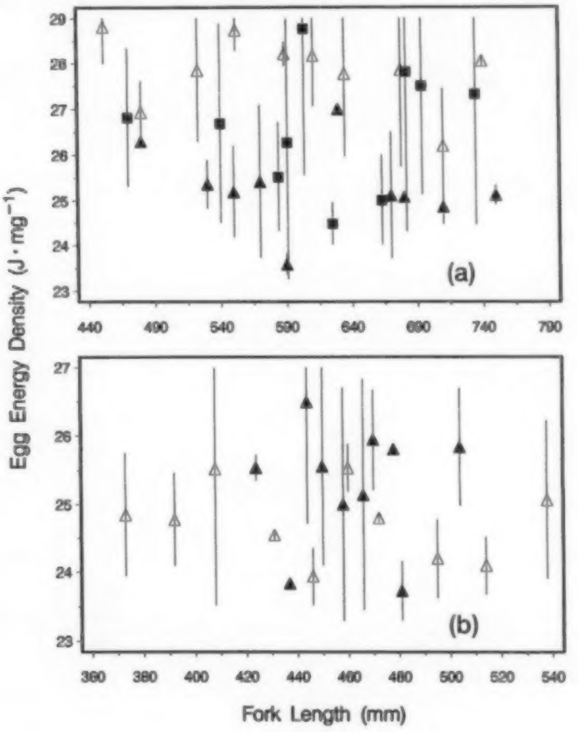


Results

Female walleye sampled from the Swan Creek spawning population ranged in size from 450 to 770 mm FL (1994, 1995, and 1996 data combined) and in age from 5 to 22 yr (1995 and 1996 data combined). The size range of sampled walleye was similar in all three years. The 28 female walleye from which eggs were fertilized to assess hatching success in 1995 ranged in size from 470 to 770 mm FL and in age from 5 to 18 yr. Female white sucker sampled from Swan Creek ranged in size from 373 to 538 mm FL (1994 and 1996 data combined) and in age from 4 to >17 yr (1996 data). A much wider size range of white sucker was sampled in 1996 than in 1994. Outer annuli on the pectoral fin rays of the three oldest white sucker in 1996 were very tightly spaced and exact ages were difficult to determine. For all three fish, at least 17 annuli were distinct, and thus, these fish were classed as >17 yr old. Dried walleye eggs were quite oily and stuck together in a brittle mass whereas dried white sucker eggs were not oily and separated easily from one another. Ash contents as a percentage of egg dry mass ranged from 3.7 to 4.8% (mean = 4.0%) for walleye (1994 and 1995 data combined) and from 3.3 to 3.8% (mean = 3.6%) for white sucker (1994 data). Ash content did not appear to vary with respect to egg dry mass.

Egg characteristics of walleye and white sucker sampled from Swan Creek are summarized in Table 1. Mean egg dry mass was higher for white sucker than for walleye in both 1994 (*t*-test, $|t| = 25.8$, df = 77, $P < 0.001$) and 1996 (*t*-test, $|t| = 14.1$, df = 73, $P < 0.001$) (Table 1). By contrast, mean egg energy density was greater for walleye than for white sucker in 1996 (*t*-test, $|t| = 10.3$, df = 18, $P < 0.001$) but not in 1994 (*t*-test, $|t| = 0.03$, $df = 18$, $P = 0.97$) (Table 1). White sucker produced

Fig. 2. Scatter plots of egg energy density versus fork length for (*a*) walleye and (*b*) white sucker females ascending Swan Creek from Lake Manitoba in 1994 (solid triangles), 1995 (solid squares), and 1996 (open triangles). Symbols represent means ± 1 SD. Note the differences in scales of axes between plots.

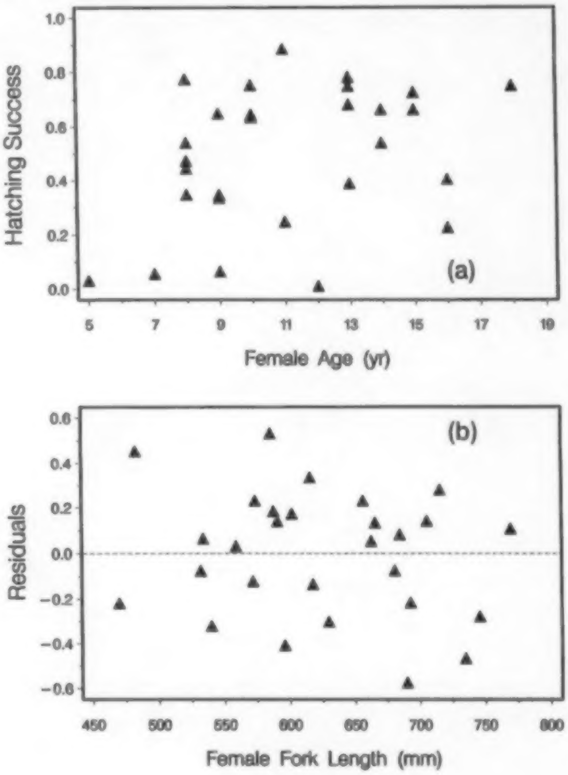


eggs of higher energy content than walleye in both 1994 (t-test, $|t| = 12.5$, df = 18, $P < 0.001$) and 1996 (t-test, $|t| = 5.1$, df = 18, $P < 0.001$) (Table 1).

The relationship between egg dry mass and female fork length for walleye was slightly curvilinear and similar between years (Fig. 1*a*). I found no interaction between the effects of $\log_e$ walleye fork length and sampling year on egg dry mass (ANCOVA, $F = 0.57$, df = 2, 114, $P = 0.57$). Walleye egg dry mass increased linearly with $\log_e$ female fork length (ANCOVA, $F = 85.7$, df = 1, 116, $P < 0.001$) and differed among years (ANCOVA, $F = 23.0$, df = 2, 116, $P < 0.001$) (Table 1). Multiple comparisons (TUKEY option, GLM procedure, SAS Institute Inc. 1985) indicated significant differences in mean egg dry mass between all years. Variation in walleye egg dry mass was explained slightly better by $\log_e$ female age ($R^2 = 0.51$) than by $\log_e$ female fork length ($R^2 = 0.47$) (1995 and 1996 data combined). Regressing egg dry mass against both $\log_e$ female fork length and $\log_e$ female age indicated that age explained a significant amount of variation in egg size that was not explained by length (ANOVA, $F = 6.63$, df = 1, 77, $P = 0.012$) but that the opposite was not true (ANOVA, $F = 0.04$, df = 1, 77, $P = 0.83$).

The relationship between egg dry mass and female fork length for white sucker differed between years (Fig. 1*b*). There was a significant interaction between the effects of $\log_e$ white sucker fork length and sampling year on egg dry mass (ANCOVA, $F = 4.18$, df = 1, 70, $P = 0.045$). White sucker egg dry mass increased linearly with $\log_e$ female fork length in 1996 (ANOVA, $F = 19.8$, df = 1, 33, $P < 0.001$, $R^2 = 0.37$) but not in 1994 (ANOVA, $F = 0.03$, df = 1, 37, $P = 0.85$, $R^2 < 0.01$). I compared white sucker egg dry mass between 1994 and 1996 using only data from the size range of females common to both years (420–510 mm FL) and found no difference between these years (t-test, $|t| = 0.59$, df = 27, $P = 0.56$) (Table 1). Variation in white sucker egg dry mass was explained slightly better by $\log_e$ female fork length ($R^2 = 0.37$) than by $\log_e$ female age ($R^2 = 0.31$) (1996 data). However, regressing egg dry mass against both $\log_e$ female fork length and $\log_e$ female age indicated that neither variable explained significant amounts of variation in egg size that was not explained by the other (ANOVA, $F < 3.9$, df = 1, 32, $P > 0.05$).

Fig. 3. Scatter plots of (*a*) egg hatching success (fraction of eggs surviving from fertilization to hatch) versus female age and (*b*) residuals from the regression of arcsine hatching success against $\log_e$ female age versus female fork length for individual broods of 28 female walleye ascending Swan Creek from Lake Manitoba in 1995.

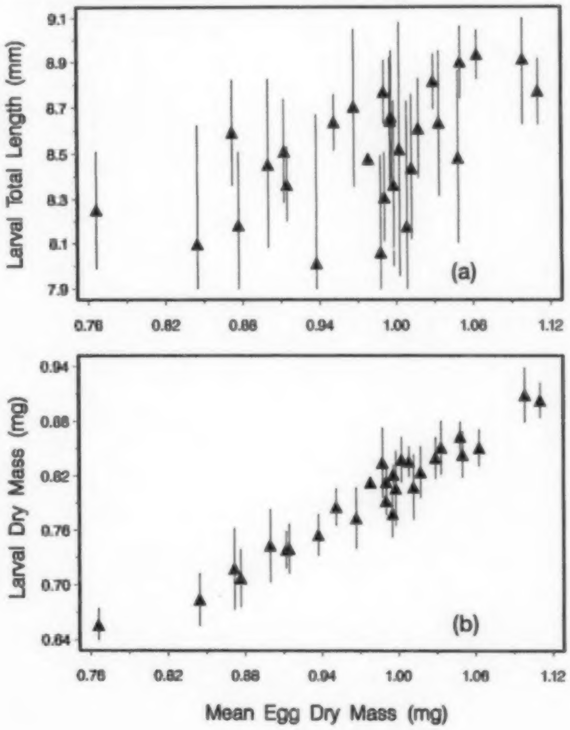


Mean egg energy densities for individual females ranged from 23.6 to 28.8 J·mg^{-1} for walleye and from 23.7 to 26.5 J·mg^{-1} for white sucker. Egg energy density showed no clear relationship with female fork length for walleye (Fig. 2*a*) or white sucker (Fig. 2*b*). There was no interaction between the effects of female fork length and sampling year on egg energy density for either walleye (ANCOVA, $F = 0.40$, df = 2, 24, $P = 0.67$) or white sucker (ANCOVA, $F = 0.13$, df = 1, 16, $P = 0.72$). In addition, there was no effect of female fork length on egg energy density for either walleye (ANCOVA, $F = 0.32$, df = 1, 26, $P = 0.57$) or white sucker (ANCOVA, $F = 0.16$, df = 1, 17, $P = 0.69$). Walleye mean egg energy density differed among years (ANOVA, $F = 15.5$, df = 2, 27, $P < 0.001$) (Table 1). Multiple comparisons (TUKEY option, GLM procedure, SAS Institute Inc. 1985) indicated significant differences in mean egg energy density between all years. White sucker mean egg energy density did not differ between years (ANOVA, $F = 2.8$, df = 1, 18, $P = 0.11$) (Table 1).

Survival from fertilization to hatch in the 28 walleye egg batches ranged from 1.1 to 88.4% (mean = 49.3%). Simple regression analyses indicated that hatching success increased linearly with $\log_e$ female age (ANOVA, $F = 4.54$, df = 1, 26, $P = 0.043$) (Fig. 3*a*) but not with either $\log_e$ female fork length (ANOVA, $F = 1.09$, df = 1, 26, $P = 0.31$) or egg dry mass (ANOVA, $F = 0.14$, df = 1, 26, $P = 0.71$). However, female fork length was able to account for some additional variation in hatching success not explained by female age (Fig. 3*b*). When hatching success was regressed against both $\log_e$ female age and $\log_e$ female fork length, there was a positive effect of female age (ANOVA, $F = 12.7$, df = 1, 25, $P = 0.0015$) and a negative effect of female fork length (ANOVA, $F = 8.45$, df = 1, 25, $P = 0.0075$). When mean egg dry mass was entered into this multiple regression model in place of female fork length, it did not account for a significant amount of residual variation (ANOVA, $F = 1.01$, df = 1, 25, $P = 0.32$). To determine if the age and fork length effects influenced survival at specific stages of incubation, I reconducted the multiple regression analyses using egg survival during the first week of incubation and egg survival from the end of the first week to hatch as dependent variables. In both cases the analysis indicated a significant positive effect of female age, a significant negative effect of female fork length, and no significant effect of egg dry mass.

Mean dry mass of larvae at hatch ranged from 78.2 to 85.6% (mean = 81.7%) of initial mean egg dry mass, and larval size at hatch was strongly dependent on initial mean egg dry mass (Fig. 4). There was a stronger relationship between larval dry mass at hatch and mean egg dry mass ($r = 0.97$) than between larval length at hatch and mean egg dry mass ($r = 0.59$) (Fig. 4).

Fig. 4. Scatter plots of (*a*) total length of larvae at hatch and (*b*) dry mass of larvae at hatch versus initial mean egg dry mass for individual broods of 28 female walleye ascending Swan Creek from Lake Manitoba in 1995. Symbols represent means ± 1 SD.



Discussion

Egg size and composition can have profound effects on the early life history of fishes. Larger walleye eggs generally have more yolk and oil and more complete essential nutrient profiles (Moodie et al. 1989). Some studies have linked large egg size with a decreased incidence of body deformities (Moodie et al. 1989), although others have found the opposite effect (Wallace and Aasjord 1984). Larger eggs give rise to larger offspring in most species (Blaxter and Hempel 1963; Fowler 1972; Gall 1974; Kazakov 1981; Elliott 1984; Thorpe et al. 1984; Wallace and Aasjord 1984; Beacham et al. 1985; Knutsen and Tilseth 1985; Rana 1985; Springate and Bromage 1985; Beacham and Murray 1986; Marsh 1986; Hinckley 1990; Hutchings 1991; reviewed by Kamler 1992; Miller et al. 1995; this study). Offspring from larger eggs have been noted to exhibit larger gapes (Knutsen and Tilseth 1985; Zastrow et al. 1989), better feeding success (Knutsen and Tilseth 1985; Moodie et al. 1989), faster growth (Wallace and Aasjord 1984), greater resistance to starvation (Blaxter and Hempel 1963; Rana 1985; Marsh 1986), and lower mortality rates (Elliott 1984; Wallace and Aasjord 1984; Hutchings 1991). Although several studies have found negligible or even negative effects of egg size on offspring quality (Fowler 1972; Lagomarsino et al. 1988; Chambers et al. 1989), most research suggests that a larger egg size conveys a significant advantage to the resultant offspring.

Virgin females generally produce the smallest eggs in spawning populations (Kamler 1992), but the relationship between egg size and female size or age appears to vary among species. Reviews by both Nikolskii (1969) and Kamler (1992) indicated that the most common relationship was dome-shaped, with the largest eggs being produced by intermediate sizes and ages of females. The observed relationship will ultimately depend on the size and age range of sampled fish relative to the size and age range of the population. Egg size shows positive relationships with female size and (or) age in numerous species (McFadden et al. 1965; de Ciechomski 1966; Wydoski and Cooper 1966; Zonova 1973; Gall 1974; DeMartini and Fountain 1981; Kazakov 1981; Rogers and Westin 1981; Elliott 1984; Thorpe et al. 1984; Mann and Mills 1985; Coates 1988; Hislop 1988; Kjesbu 1989; Zastrow et al. 1989; Fleming and Gross 1990; Buckley et al. 1991; Parker and Franzin

1991). Fewer studies have reported no clear relationship between egg size and female size or age (Wolfert 1969; Serns 1982; Townshend and Wootton 1984; Chambers et al. 1989; Hinckley 1990; Trippel 1993) or a negative relationship (Broussard and Stickney 1981).

I observed positive relationships between the dry mass of walleye eggs and the size and age of the female. Female age accounted for a greater amount of variation in egg mass than fork length. The shape of these relationships appeared to be curvilinear, with egg size increasing at a decelerating rate with respect to female length or age. It is possible that egg mass declines with female size or age in walleye larger than those sampled in this study. However, female walleye of larger size appear to form a minor component of most spawning populations (Wolfert 1969; Forney 1976; Serns 1982; Mathias et al. 1985), possibly because few females live to attain such sizes or because older females become senescent or fail to spawn annually (Deason 1933; Carlander 1945). Because the most rapid change in egg size in relation to female size was evident in the smallest fish, the egg size versus female size relationship may be stronger in populations composed of smaller females. Mature female walleye of <500 mm FL were uncommon in the Swan Creek spawning population but are common in some other populations (e.g., Serns 1982; Mathias et al. 1985). In contrast with walleye, I found a positive relationship between egg dry mass and fork length of female white sucker in 1996 but not in 1994. However, the difference in this relationship between years may be attributable to the restricted size range of females sampled in 1994.

I found considerable among-female variation in the egg energy densities of both walleye and white sucker. This would be expected given the among-female variation in egg proximate composition seen in other species (Zastrow et al. 1989). However, variation in egg energy density did not appear to be related to the size of the female. Mean energy densities and energy contents of walleye and white sucker eggs as estimated in this study were somewhat higher than those reported for eggs of demersal-spawning marine species (Hislop and Bell 1987; Kamler 1992). Eggs containing oil globules, such as walleye eggs, are generally more energy dense than those lacking an oil globule, such as white sucker eggs (Hislop and Bell 1987). I had expected to observe a higher energy density for walleye eggs than for white sucker eggs, but this trend was not consistent between years. However, white sucker eggs had a consistently higher energy content than walleye eggs. The greater energy content of white sucker eggs may allow white sucker larvae to delay initial feeding for longer than walleye larvae. Walleye larvae typically leave the spawning bed immediately after hatching whereas white sucker larvae remain in the gravel for 1–2 wk before moving to nursery areas (Corbett and Powles 1986).

Variation in egg size and composition among females of a single population may be attributed to a number of factors other than female size or age. Egg size of individual females varies over the spawning season in batch-spawning species (DeMartini and Fountain 1981; Kjesbu 1989; Hinckley 1990; Buckley et al. 1991; Kjesbu et al. 1991). As most of the energy used in ovarian growth comes from the muscle and liver (Kjesbu et al. 1991; Kamler 1992; Wiegand 1996), the trend of decreasing egg size over the spawning season probably reflects a depletion of somatic reserves. Thus, egg quality should, intuitively, be related to some measure of female nutritional state such as condition, growth rate, or food abundance. However, the effects appear to be variable and may be species specific (reviewed by Kamler 1992). Bagenal (1969) reported that well-fed, fast-growing female brown trout (*Salmo trutta*) produced more eggs and eggs of lower dry mass than poorly fed, slow-growing fish of the same size. In contrast, higher food intake, faster growth, and high female condition during oogenesis may lead to production of larger or more energy-rich eggs in other species (Nikolskii 1969; Hay and Brett 1988; Chambers et al. 1989). This may explain why hatchery-reared broodstock generally produce larger eggs than their wild conspecifics (Fleming and Gross 1990). Much of the egg size and energy density variation observed in this study was not explained by female size or age and may have been due to nutritional state or genetic variation.

Egg quality also varies among populations of a species (Marsh 1984; Thresher 1988; Fleming and Gross 1990; Kamler 1992) and within a population among years (Mann and Mills 1985; Kamler 1992; Sarvala and Helminen 1995). Walleye eggs collected in this study were somewhat heavier than walleye eggs collected from Crean Lake, Saskatchewan (range 0.73–0.81 mg mean dry mass) (Moodie et al. 1989). However, the Crean Lake spawning population was composed of smaller females (Mathias et al. 1985). Mean dry mass of white sucker (370–470 mm FL) eggs in five Ontario lakes ranged from 1.86 to 2.34 mg and varied among populations (Trippel and Harvey 1987). White sucker eggs collected in this study were considerably lighter. I also observed a significant difference in walleye egg dry mass among years. Interannual variation in egg size has been linked to variation in year-class strength of coregonids (Sarvala and Helminen 1995). Interpopulation and interannual variation in egg quality presumably results from the same factors influencing intrapopulation variability, such as feeding conditions or genetics. It has been suggested that the proportion of mature females producing eggs and spawning each spring may be related to the previous season's somatic growth and female energy reserves for both walleye (Forney 1965; Henderson et al. 1996) and white sucker (Trippel and Harvey 1989). Somatic growth and energy reserves may also affect walleye egg size but, this has yet to be investigated. Interpopulation variation in egg size of white sucker has also been linked to environmental changes accompanying acid stress (Trippel and Harvey 1987) and metal pollution (McFarlane and Franzin 1978; Munkittrick and Dixon 1988).

I found that the hatching success of walleye eggs was positively related to female age and negatively related to female length adjusted for age. Kamler (1992) suggested that survival is usually greatest for the eggs of intermediate-aged fish. This was not apparent for walleye. Auer and Auer (1987) found a negative relationship between walleye egg survival and female size. However, comparisons between their results and my own are difficult because they examined few fish ($n = 4$), incubated at a warmer temperature (range 13–18°C) and did not analyze their data with respect to both female size and age. Previous studies have found positive effects of female size (Zastrow et al. 1989; Buckley et al. 1991), negative effects of female size (Beacham and Murray 1985), and positive effects of female age (Gall 1974; Pitman 1979) on egg hatching success in other species. I found no effect of egg size on egg survival, a result consistent with earlier research (Zonova 1973; Broussard and Stickney 1981; Thorpe et al. 1984; Springate and Bromage 1985; Docker et al. 1986; Moodie et al. 1989; Hutchings 1991). My results suggest that older walleye and walleye of smaller size at age will produce eggs having a higher survival independent of egg size. The eggs of such females may contain greater amounts of some limiting nutrient. For example, survival of rainbow trout (*Oncorhynchus mykiss*) eggs was found to be positively related to egg protein content (Satia et al. 1974).

The results of my walleye egg hatching success study should be considered with respect to natural conditions. I incubated all egg batches at 12°C, but eggs of individual females may experience quite different temperature regimes from one another in nature. Walleye may spawn over several weeks (Colby et al. 1979), and eggs spawned early would incubate, on average, at lower temperatures than those spawned late. In the Swan Creek spawning stock, larger female walleye tend to spawn earlier than smaller females (D. Carson, Manitoba Department of Natural Resources, Fisheries Branch, Winnipeg, Man., personal communication). Thus, an interactive effect of female size and (or) age and water temperature on egg survival may exist and should be investigated further.

My results indicate that egg mass varies with respect to female size and age in walleye and possibly white sucker of Lake Manitoba. Furthermore, walleye egg survival varies with respect to female size and age. Thus, the egg quality of these species in Lake Manitoba could vary with changes in the size or age structure of their populations. These findings have implications for fisheries management. Exploitation tends to remove older individuals and frequently causes faster growth, earlier age of maturity (reviewed by Trippel 1995), and increased fecundity (Healey 1978; Baccante and Reid 1988) in fish stocks. Faster growth may in turn reduce the natural lifespan (Craig 1985). Thus, exploitation shifts egg production from relatively old, slow-growing females to relatively young, fast-growing females and may result in the production of smaller, less viable eggs. This may lead to reduced spawning success and the formation of weak year-classes. These potential consequences of changing egg quality should be investigated further and considered in future population models and management plans.

Acknowledgements

I thank the staff of the Manitoba Department of Natural Resources' Fish Culture Section and the Swan Creek hatchery for allowing me to collect samples during their spawn-taking operations. I was assisted in the field by Karen Broughton, Rob Cann, Don Carson, Rob Currie, Aaron Fisk, and Lenore Vandenbyllaardt. Rick Wastle determined fish ages and Mike Giles assisted with the egg incubation system. John Babaluk, Mike Giles, Jack Mathias, Don Metner, Ken Mills, Ron Schade, and Fred Ward kindly allowed me to use their equipment and (or) laboratory space. Karen Broughton, Pierre Pepin, Ken Stewart, and Ed Trippel provided constructive criticisms on earlier drafts of this manuscript. Operating expenses were supported by grants from Fish Futures Manitoba and Manitoba Hydro. Much of this research was conducted while I was supported by a Canadian Government Laboratory Visiting Fellowship through the Department of Fisheries and Oceans' Habitat Action Plan.

References

Auer, N.A., and Auer, M.T. 1987. Field evaluation of barriers to walleye egg and larva survival in the Lower Fox River, Wisconsin. Am. Fish. Soc. Symp. **2**: 93–101.

Baccante, D.A., and Reid, D.M. 1988. Fecundity changes in two exploited walleye populations. N. Am. J. Fish. Manage. **8**: 199–209.

Bagenal, T.B. 1969. The relationship between food supply and fecundity in brown trout *Salmo trutta* L. J. Fish Biol. **1**: 167–182.

Bagenal, T.B. 1971. The interrelation of the size of fish eggs, the date of spawning and the production cycle. J. Fish Biol. **3**: 207–219.

Beacham, T.D., and Murray, C.B. 1985. Effect of female size, egg size, and water temperature on developmental biology of chum salmon (*Oncorhynchus keta*) from the Nitinat River, British Columbia. Can. J. Fish. Aquat. Sci. **42**: 1755–1765.

Beacham, T.D., and Murray, C.B. 1986. Comparative developmental biology of chum salmon (*Oncorhynchus keta*) from the Fraser River, British Columbia. Can. J. Fish. Aquat. Sci. **43**: 252–262.

Beacham, T.D., Withler, F.C., and Morley, R.B. 1985. Effect of egg size on incubation time and alevin and fry size in chum salmon (*Oncorhynchus keta*) and coho salmon (*Oncorhynchus kisutch*). Can. J. Zool. **63**: 847–850.

Blaxter, J.H.S., and Hempel, G. 1963. The influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons. Int. Explor. Mer, **28**: 211–240.

Broussard, M.C. Jr., and Stickney, R.R. 1981. Evaluation of reproductive characters for four strains of channel catfish. Trans. Am. Fish. Soc. **110**: 502–506.

Buckley, L.J., Smigielski, A.S., Halavik, T.A., Caldarone, E.M., Burns, B.R., and Laurence, G.C. 1991. Winter flounder *Pseudopleuronectes americanus* reproductive success. II. Effects of spawning time and female size on size, composition and viability of eggs and larvae. Mar. Ecol. Prog. Ser. **74**: 125–135.

Carlander, K.D. 1945. Age, growth, sexual maturity, and populations of the yellow pike-perch, *Stizostedion vitreum vitreum* (Mitchill), with reference to the commercial fisheries, Lake of the Woods, Minnesota. Trans. Am. Fish. Soc. **73**: 90–107.

Chambers, R.C., Leggett, W.C., and Brown, J.A. 1989. Egg size, female effects, and the correlations between early life history traits of capelin, *Mallotus villosus*: an appraisal at the individual level. Fish. Bull. U.S. **87**: 515–523.

Chilton, D.E., and Beamish, R.J. 1982. Age determination methods for fishes studied by the Groundfish Program at the Pacific Biological Station. Can. Spec. Publ. Fish. Aquat. Sci. No. 60.

Coates, D. 1988. Length-dependent changes in egg size and fecundity in females, and brooded embryo size in males, of fork-tailed catfishes (Pisces: Ariidae) from the Sepik River, Papua New Guinea, with some implications for stock assessments. J. Fish Biol. **33**: 455–464.

Colby, P.J., and Nepszy, S.J. 1981. Variation among stocks of walleye (*Stizostedion vitreum vitreum*): management implications. Can. J. Fish. Aquat. Sci. **38**: 1814–1831.

Colby, P.J., McNicol, R.E., and Ryder, R.A. 1979. Synopsis of biological data on the walleye *Stizostedion v. vitreum* (Mitchill 1818). FAO Fish. Synop. 119.

Corbett, B.W., and Powles, P.M. 1986. Spawning and larva drift of sympatric walleyes and white suckers in an Ontario stream. Trans. Am. Fish. Soc. **115**: 41–46.

Craig, J.F. 1985. Aging in fish. Can. J. Zool. **63**: 1–8.

Craig, J.F., Babaluk, J.A., Stevenson, S.G., and Williams, P.C. 1995. Variation in growth and reproduction of walleye (*Stizostedion vitreum*) in three Manitoba lakes. Can. J. Zool. **73**: 367–372.

Deason, H.J. 1933. Preliminary report on the growth rate, dominance, and maturity of the pike-perches (*Stizostedion*) of Lake Erie. Trans. Am. Fish. Soc. **63**: 348–360.

de Ciechomski, J.Dz. 1966. Development of the larvae and variations in the size of the eggs of the Argentine anchovy, *Engraulis* *anchoita* Hubbs and Marini. J. Cons. Cons. Int. Explor. Mer, **30**: 281–290.

DeMartini, E.E., and Fountain, R.K. 1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: attributes representative of serial spawning fishes. Fish. Bull. U.S. **79**: 547–560.

Docker, M.F., Medland, T.E., and Beamish, F.W.H. 1986. Energy requirements and survival in embryo mottled sculpin (*Cottus bairdi*). Can. J. Zool. **64**: 1104–1109.

Elliott, J.M. 1984. Numerical changes and population regulation in young migratory trout *Salmo trutta* in a lake district stream, 1966–83. J. Anim. Ecol. **53**: 327–350.

Fleming, I.A., and Gross, M.R. 1990. Latitudinal clines: a trade-off between egg number and size in Pacific salmon. Ecology, **71**: 1–11.

Forney, J.L. 1965. Factors affecting growth and maturity in a walleye population. N.Y. Fish Game J. **12**: 217–232.

Forney, J.L. 1976. Year-class formation in the walleye (*Stizostedion vitreum vitreum*) population of Oneida Lake, New York, 1966–73. J. Fish. Res. Board Can. **33**: 783–792.

Fowler, L.G. 1972. Growth and mortality of fingerling chinook salmon as affected by egg size. Prog. Fish-Cult. **34**: 66–69.

Fuiman, L.A., and Trojnar, J.R. 1980. Factors affecting egg diameter of white suckers (*Catostomus commersoni*). Copeia, **1980**: 699–704.

Gall, G.A.E. 1974. Influence of size of eggs and age of female on hatchability and growth in rainbow trout. Calif. Fish Game, **60**: 26–35.

Hay, D.E., and Brett, J.R. 1988. Maturation and fecundity of Pacific herring (*Clupea harengus pallasi*): an experimental study with comparisons to natural populations. Can. J. Fish. Aquat. Sci. **45**: 399–406.

Healey, M.C. 1978. Fecundity changes in exploited populations of lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. **35**: 945–950.

Henderson, B.A., Wong, J.L., and Nepszy, S.J. 1996. Reproduction of walleye in Lake Erie: allocation of energy. Can. J. Fish. Aquat. Sci. **53**: 127–133.

Hinckley, S. 1990. Variation of egg size of walleye pollock *Theragra chalcogramma* with a preliminary examination of the effect of egg size on larval size. Fish. Bull. U.S. **88**: 471–483.

Hislop, J.R.G. 1988. The influence of maternal length and age on the size and weight of the eggs and the relative fecundity of the haddock, *Melanogrammus aeglefinus*, in British waters. J. Fish. Biol. **32**: 923–930.

Hislop, J.R.G., and Bell, M.A. 1987. Observations on the size, dry weight and energy content of the eggs of some demersal fish species from British marine waters. J. Fish Biol. **31**: 1–20.

Hutchings, J.A. 1991. Fitness consequences of variation in egg size and food abundance in brook trout *Salvelinus fontinalis*. Evolution, **45**: 1162–1168.

Johnston, T.A., Gaboury, M.N., Janusz, R.A., and Janusz, L.R. 1995. Larval fish drift in the Valley River, Manitoba: influence of abiotic and biotic factors, and relationships with future year-class strengths. Can. J. Fish. Aquat. Sci. **52**: 2423–2431.

Kamler, E. 1992. Early life history of fish: an energetics approach. Chapman and Hall, London.

Kazakov, R.V. 1981. The effect of the size of Atlantic salmon, *Salmo salar* L., eggs on embryos and alevins. J. Fish Biol. **19**: 353–360.

Kjesbu, O.S. 1989. The spawning activity of cod, *Gadus morhua* L. J. Fish Biol. **34**: 195–206.

Kjesbu, O.S., Klungsoyr, J., Kryvi, H., Witthames, P.R., and Greer Walker, M. 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Can. J. Fish. Aquat. Sci. **48**: 2333–2343.

Knutsen, G.M., and Tilseth, S. 1985. Growth, development, and feeding success of Atlantic cod larvae *Gadus morhua* related to egg size. Trans. Am. Fish. Soc. **114**: 507–511.

Koenst, W.M., and Smith, L.L. Jr. 1976. Thermal requirements of the early life history stages of walleye, *Stizostedion vitreum*, and sauger, *Stizostedion canadense*. J. Fish. Res. Board Can. **33**: 1130–1138.

Lagomarsino, I.V., Francis, R.C., and Barlow, G.W. 1988. The lack of correlation between size of egg and size of hatchling in the Midas cichlid (*Cichlasoma citrinellum*). Copeia, **1988**: 1086–1089.

Mann, R.H.K., and Mills, C.A. 1985. Variations in the sizes of gonads, eggs and larvae of the dace, *Leuciscus leuciscus*. Environ. Biol. Fishes, **13**: 277–287.

Marsh, E. 1984. Egg size variation in central Texas populations of *Etheostoma spectabile* (Pisces: Percidae). Copeia, **1984**: 291–301.

Marsh, E. 1986. Effects of egg size on offspring fitness and maternal fecundity in the orangethroat darter, *Etheostoma spectabile* (Pisces: Percidae). Copeia, **1986**: 18–30.

Mathias, J.A., Babaluk, J.A., and Rowes, K.D. 1985. An analysis of the 1984 walleye, *Stizostedion vitreum vitreum* (Mitchill), run at Crean Lake in Prince Albert National Park, Saskatchewan with reference to the impact of spawn-taking. Can. Tech. Rep. Fish. Aquat. Sci. No. 1407.

McFadden, J.T., Cooper, E.L., and Andersen, J.K. 1965. Some effects of environment on egg production in brown trout (*Salmo trutta*). Limnol. Oceanogr. **10**: 88–95.

McFarlane, G.A., and Franzin, W.G. 1978. Elevated heavy metals: a stress on a population of white suckers, *Catostomus commersoni*, in Hamell Lake, Saskatchewan. J. Fish. Res. Board Can. **35**: 963–970.

Miller, T.J., Herra, T., and Leggett, W.C. 1995. An individual-based analysis of the variability of eggs and their newly hatched larvae of Atlantic cod (*Gadus morhua*) on the Scotian shelf. Can. J. Fish. Aquat. Sci. **52**: 1083–1093.

Moodie, G.E.E., Loadman, N.L., Wiegand, M.D., and Mathias, J.A. 1989. Influence of egg characteristics on survival, growth, and feeding in larval walleye (*Stizostedion vitreum*). Can. J. Fish. Aquat. Sci. **46**: 516–521.

Moore, A.A. 1987. Short-term storage and cryopreservation of walleye semen. Prog. Fish-Cult. **49**: 40–43.

Munkittrick, K.R., and Dixon, D.G. 1988. Growth, fecundity, and energy stores of white sucker (*Catostomus commersoni*) from lakes containing elevated levels of copper and zinc. Can. J. Fish. Aquat. Sci. **45**: 1355–1365.

Nikolskii, G.V. 1969. Theory of fish population dynamics as the biological background for rational exploitation and management of fishery resources. Oliver and Boyd, Edinburgh.

Parker, B.R., and Franzin, W.G. 1991. Reproductive biology of the quillback, *Carpiodes cyprinus*, in a small prairie river. Can. J. Zool. **69**: 2133–2139.

Pitman, R.W. 1979. Effects of female age and egg size on growth and mortality in rainbow trout. Prog. Fish-Cult. **41**: 202–204.

Prus, T. 1975. Measurement of calorific value using Phillipson microbomb calorimeter. *In* Methods for ecological bioenergetics. *Edited by* W. Grodzinski, R.Z. Klekowski, and A. Duncan. Blackwell Scientific Publications, Oxford. pp. 149–160.

Rana, K.J. 1985. Influence of egg size on the growth, onset of feeding, point-of-no-return, and survival of unfed *Oreochromis mossambicus* fry. Aquaculture, **46**: 119–131.

Rogers, B.A., and Westin, D.T. 1981. Laboratory studies on effects of temperature and delayed initial feeding on development of striped bass larvae. Trans. Am. Fish. Soc. **110**: 100–110.

Sarvala, J., and Helminen, H. 1995. Significance of egg size variation in the year-class fluctuations of vendace (*Coregonus albula*). Arch. Hydrobiol. Spec. Issues Adv. Limnol. **46**: 187–194.

SAS Institute Inc. 1985. SAS user's guide: version 5 edition. SAS Institute Inc., Cary, N.C.

Satia, B.P., Donaldson, L.R., Smith, L.S., and Nightingale, J.N. 1974. Composition of ovarian fluid and eggs of the University of Washington strain of rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. **31**: 1796–1799.

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. No. 184.

Serns, S.L. 1982. Walleye fecundity, potential egg deposition, and survival from egg to fall young-of-year in Escanaba Lake, Wisconsin, 1979–1981. N. Am. J. Fish. Manage. **4**: 388–394.

Springate, J.R.C., and Bromage, N.R. 1985. Effects of egg size on early growth and survival in rainbow trout (*Salmo gairdneri* Richardson). Aquaculture, **47**: 163–172.

Thorpe, J.E., Miles, M.S., and Keay, D.S. 1984. Developmental rate, fecundity and egg size in Atlantic salmon, *Salmo salar* L. Aquaculture, **43**: 289–305.

Thresher, R.E. 1988. Latitudinal variation in egg sizes of tropical and sub-tropical North Atlantic shore fishes. Environ. Biol. Fishes, **21**: 17–25.

Townshend, T.J., and Wootton, R.J. 1984. Effects of food supply on the reproduction of the convict cichlid, *Cichlasoma nigrofasciatum*. J. Fish Biol. **24**: 91–104.

Trippel, E.A. 1993. Relations of fecundity, maturation, and body size of lake trout, and implications for management in northwestern Ontario lakes. N. Am. J. Fish. Manage. **13**: 64–72.

Trippel, E.A. 1995. Age at maturity as a stress indicator in fisheries. Bioscience, **45**: 759–771.

Trippel, E.A., and Harvey, H.H. 1987. Reproductive responses of five white sucker (*Catostomus commersoni*) populations in relation to lake acidity. Can. J. Fish. Aquat. Sci. **44**: 1018–1023.

Trippel, E.A., and Harvey, H.H. 1989. Missing opportunities to reproduce: an energy dependent or fecundity gaining strategy in white sucker (*Catostomus commersoni*). Can. J. Zool. **67**: 2180–2188.

Wallace, J.C., and Aasjord, D. 1984. An investigation of the consequences of egg size for the culture of Arctic charr, *Salvelinus alpinus* (L.). J. Fish Biol. **24**: 427–435.

Waltemyer, D.L. 1976. Tannin as an agent to eliminate adhesiveness of walleye eggs during artificial propagation. Trans. Am. Fish. Soc. **105**: 731–736.

Wiegand, M.D. 1996. Composition, accumulation and utilization of yolk lipids in teleost fish. Rev. Fish Biol. Fish. **6**: 259–286.

Wolfert, D.R. 1969. Maturity and fecundity of walleyes from the eastern and western basins of Lake Erie. J. Fish. Res. Board Can. **26**: 1877–1888.

Wydoski, R.S., and Cooper, E.L. 1966. Maturation and fecundity of brook trout from infertile streams. J. Fish. Res. Board Can. **23**: 623–649.

Zastrow, C.E., Houde, E.D., and Saunders, E.H. 1989. Quality of striped bass (*Morone saxatilis*) eggs in relation to river source and female weight. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **191**: 34–42.

Zonova, A.S. 1973. The connection between egg size and some of the characters of female carp (*Cyprinus carpio*). J. Ichthyol. **13**: 679–689.

Effects of a fluctuation in Fraser River discharge on primary production in the central Strait of Georgia, British Columbia, Canada

Kedong Yin, Paul J. Harrison, and Richard J. Beamish

Abstract: High-resolution vertical profiles of salinity, temperature, fluorescence, and nutrients (NO_3 and SiO_4) were taken along a transect in the central Strait of Georgia, British Columbia. The Fraser River discharge increased rapidly over 4 days and then decreased over the following 3 days (June 16–19, 1991). The thickness and extent of the estuarine plume increased as a response to the increased river discharge. As the estuarine plume flowed seaward, the nutricline (NO_3) became shallower and broader, resulting in an increase in NO_3 in the euphotic zone. Entrainment of NO_3 may explain the increase in NO_3 in the surface layer, and the amount of NO_3 entrained was estimated to be 5–10 times higher than river-borne NO_3. The utilization of entrained nutrients increased Chl *a* concentrations and primary production to levels comparable with spring bloom values. Our results clearly demonstrated for the first time that entrainment of nutrients and phytoplankton production in the central Strait of Georgia are closely coupled to fluctuations in the Fraser River discharge as the estuarine plume moves seaward. The timing and magnitude of the May–June freshet could control the entrainment of nutrients and thus maintain high primary productivity in late spring – early summer.

Résumé : Des profils verticaux haute résolution de la salinité, de la température, de la fluorescence et d'éléments nutritifs (NO_3 et SiO_4) ont été obtenus le long d'un transect au centre du détroit de Georgia, en Colombie-Britannique. Le débit du fleuve Fraser a augmenté rapidement pendant 4 jours, puis a diminué au cours des 3 jours suivants (du 16 au 19 juin 1991). L'épaisseur et la taille du panache estuarien ont augmenté en réaction à l'augmentation du débit du fleuve. Au fur et à mesure que le panache s'est dirigé vers la mer, la nutricline (NO_3) est devenue moins profonde et plus large, entraînant une augmentation de la concentration de NO_3 dans la zone euphotique. L'entraînement du NO_3 peut expliquer l'augmentation de sa concentration dans la couche superficielle et la quantité de NO_3 entraîné a été estimée à 5–10 fois celle qui est transportée par le fleuve. L'utilisation des éléments nutritifs entraînés a augmenté la concentration de Chl *a* et la production primaire à des niveaux comparables à ceux qui sont observés au cours des proliférations printanières. Nos résultats ont clairement démontré pour la première fois que l'entraînement des éléments nutritifs et la production de phytoplancton dans le centre du détroit de Georgia sont étroitement liés aux fluctuations du débit du fleuve Fraser, avec le déplacement du panache en direction de la mer. Les concentrations élevées d'éléments nutritifs et la production élevée de phytoplancton à la fin du printemps et au début de l'été peuvent être maintenues par l'entraînement. Le moment et l'importance de la crue nivale de mai–juin pourraient régir l'entraînement des éléments nutritifs et, ainsi, maintenir la productivité primaire élevée de la fin du printemps et du début de l'été.

[Traduit par la Rédaction]

Introduction

Entrainment is one of most important mixing processes in estuaries (Mann and Lazier 1991). However, there are few direct observations on the dynamics of nutrients associated with mixing processes caused by entrainment. The Gulf of St. Lawrence estuary is a well-known example for entrainment of nutrients. Intensive entrainment occurs at the head of the Laurentian Channel (Ingram 1979) and was suggested to play an important role in nutrient supply by acting as a "nutrient pump" for enhancing biological production in the Gaspé Current (Steven 1974; Therriault and Lacroix 1976). This entrained nutrient source was reported to represent more than 75% of the total nutrient supply to the euphotic zone in the estuary, the remainder (<25%) being of freshwater origin (Greisman and Ingram 1977). However, this estimate has been questioned by Sinclair et al. (1976), who stated that the magnitude of the nutrient pump and the estuarine nutrient transport have an impact on a much smaller geographical area. Even in the St. Lawrence River estuary, there has been no direct observation of entrainment that can occur daily at the halocline over the entire estuary as its surface estuarine plume flows seaward. In coastal oceans where estuaries discharge onto the continental shelf, it has been shown that deeper waters are drawn towards the mouth of the estuary such as Chesapeake Bay (Norcross and Stanley 1967) and Delaware Bay (Pape and Garvine 1982). It is therefore reasonable to assume that nutrients in the deep water are eventually entrained into the estuarine plume. Direct evidence of the magnitude of this entrainment is lacking (Mann and Lazier 1991).

In many estuarine systems, dynamics of nutrients and phytoplankton biomass are mainly determined by the balance between

Received February 12, 1996. Accepted October 7, 1996.
J13297

K. Yin[1] and P.J. Harrison. Department of Oceanography, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.
R.J. Beamish. Pacific Biological Station, Department of Fisheries and Oceans, Nanaimo, BC V9R 5K6, Canada.

[1] Author to whom all correspondence should be addressed. e-mail: kedong@unixg.ubc.ca; pharrisn@unixg.ubc.ca

Can. J. Fish. Aquat. Sci. **54**: 1015–1024 (1997)

dilution by river runoff and phytoplankton growth because freshwaters usually have high concentrations of nutrients relative to their adjacent seawater (e.g., San Francisco Bay estuary (Cloern et al. 1983), Chesapeake Bay and Delaware and Hudson estuaries (Fisher et al. 1988)). However, concentrations of inorganic nitrogen in the Fraser River during late spring and summer are not sufficient to allow blooms after dilution with the nutrient-depleted surface water from the Strait of Georgia (Yin et al. 1995*a*). Early studies by Parsons et al. (1970, see their Fig. 1) and Stockner et al. (1979, see their Table 1) suggested that phytoplankton biomass and production starts to decrease rapidly in May after the spring bloom. In contrast, recent investigations in the Strait of Georgia estuary (Clifford et al. 1990; Harrison et al. 1991) indicated blooms in June and July during the annual maximum river discharge. Entrainment of nutrients due to the maximum river discharge has been proposed to be the major mechanism for maintaining high primary production after the spring bloom (Harrison et al. 1983).

The Fraser River discharge starts to increase in March, reaches a maximum (up to 10 000 $m^3 \cdot s^{-1}$) in June, gradually decreases in July, August, and September, and then remains near the minimum levels (down to 700 $m^3 \cdot s^{-1}$) throughout the rest of the year. The daily freshwater outflow in the Fraser River is tidally modulated, being dammed during tidal floods and released during tidal ebbs. When the Fraser River outflow is released during ebb tides, it forms the riverine plume in the Strait. The extent of the riverine plume depends on the tidal stage, the amount of freshwater outflow, and winds. The riverine plume is mixed with saltier water by winds and the mixture becomes the estuarine plume. The estuarine plume extends over most of the central and southern region of the Strait and builds up a surface slope in the Strait of Georgia towards the Juan de Fuca Strait (Waldichuk 1957). The surface layer will entrain seawater from below as it moves seaward over the lower layer (Cordes et al. 1980). Previous studies have been focused on the direct entrainment of nutrients by the riverine plume at the river mouth (Yin et al. 1995*a*, 1995*b*, 1995*c*). Direct entrainment near the river mouth by the riverine plume was observed to depend on the magnitude of the river discharge; the amount of entrained NO_3 increased as the river discharge increased (Yin et al. 1995*b*). As shown in the same study, the high river discharge pushed the nitrogen-depleted estuarine plume seaward. The seaward movement of the estuarine plume driven by the maximal river discharge is hypothesized to result in entrainment of nutrients from the deep water in the central part of the Strait of Georgia. However, this effect has never been clearly demonstrated in the central Strait due to the lack of detailed high-resolution profiles. Also, no observations have been made on the response of phytoplankton biomass and productivity to entrained nutrients.

There are different water masses and flows that are complex in estuaries. Temporal fluctuations are also large. The time scale for sampling in most studies is often insufficient to examine day-to-day variation. Point samples are usually used to obtain vertical profiles of nutrients in the water column, but they provide inadequate resolution to relate nutrients to physical mixing processes.

In this study, we examined day-to-day variations of salinity, temperature, fluorescence, and nutrients in the water column using high-resolution vertical profiles. Such an examination of day-to-day variations has proven to be important in understanding the coupling of biological processes to physical processes (Bailey and Chapman 1991; Pitcher et al. 1991; Yin et al. 1996). Also, high-resolution vertical profiles of physical and biological variables in this study were plotted together to see how they related to each other. The cruise period was in June during high river discharge and the spatial scale was at the mesoscale level (>100 km) in the central Strait of Georgia. By sampling the transect daily during the cruise, we were able to observe how biological variables such as nutrients and phytoplankton biomass responded to changes in physical variables induced by an increase in river discharge. The intent of this study was to fill the gap in knowledge of entrainment of nutrients by the estuarine plume; this gap became apparent during development of the conceptual model in the previous study (Yin et al. 1995*a*, 1995*b*). The objectives were to examine if the entrainment of nutrients in the estuarine plume occurred and how it responded to the change in magnitude of the Fraser River discharge. We also assessed how important the amount of entrained NO_3 was compared with river-borne NO_3 and determined if phytoplankton production responded to entrained nutrients.

Materials and methods

Station locations

The transect started from station S2 near the river mouth (8 km away) to S1 (108 km) in the northwest direction, covering most of the central Strait (Fig. 1). Strictly speaking, there is no upper or lower estuary, since the outflow of the Fraser River depends mainly on the direction of the wind (LeBlond 1983). In general, however, since the outflow moves northward due to the Coriolis effect, the direction from stations S2 through P1, S3, P2–P7 to S1 is similar to the seaward direction in an estuary. Therefore, this northwestward direction is referred to as "seaward" in this study. The station numbers are consistent with previous studies (Yin et al. 1995*a*, 1995*b*, 1995*c*, 1996). The sampling strategy was to investigate the distribution of nutrients associated with the movement of the estuarine plume.

Sampling and data processing

At each station, a vertical profile (0–25 m) of temperature, salinity, in vivo fluorescence, and selected nutrients ($NO_3 + NO_2$, NH_4, PO_4, and SiO_4) was obtained. The vertical profiling system has been described in detail by Jones et al. (1991) and Yin et al (1995*a*). Basically, a hose connected to a water pump on deck was attached to an S4 current meter (InterOcean®) that also contained a CTD probe. The hose and the CTD probe were lowered slowly into the water at 1 $m \cdot min^{-1}$ and water was pumped into a fluorometer and an AutoAnalyzer® onboard for in vivo Chl *a* fluorescence and nutrient measurements, respectively. Each sampling produced a high-resolution continuous vertical profile of those physical and biological parameters, and thus the relationship between those parameters in the water column could be easily recognized.

Data from a vertical profile were smoothed over 0.5-min intervals. This smoothing reduced the fluctuations caused by the ship's motion.

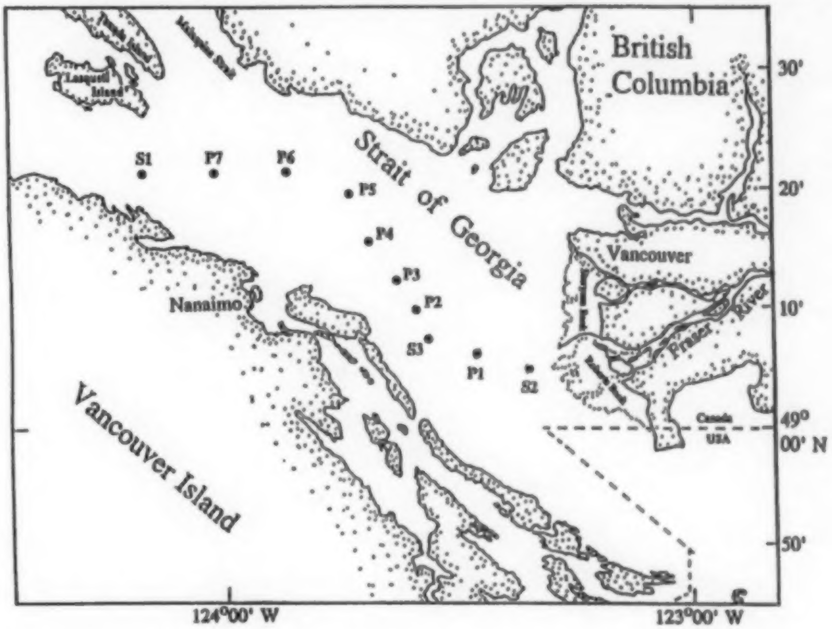
The Practical Salinity Scale was used in the text and figures for salinity measurement. Therefore, the salinity values have no units but they are equivalent to parts per thousand (Pond and Pickard 1978).

Nutrient analysis

All nutrients were determined using a Technicon AutoAnalyzer® II. Salinity effects on nutrient analyses were tested onboard ship and were found to be small over the range of salinities in the estuary. Therefore, no correction was made for salinity effects.

NO_3 (+NO_2) and NH_4 were determined following the procedures

Fig. 1. Map of the study area and the stations in the vicinity of the Fraser River plume. The transect starts at station S2 near the river mouth (8 km away) and goes to station S1 (108 km away) in the northwestward direction, covering most of the central Strait of Georgia.



of Wood et al. (1967) and Slawyk and MacIsaac (1972), respectively. SiO_4 was determined following Armstrong et al. (1967), and PO_4 was determined according to Hager et al. (1968).

Primary production and Chl *a*

The measurement of incident solar irradiance (PAR) and subsurface light intensities and the collection of water samples for ^{14}C uptake experiments and nutrients were described by Harrison et al. (1991). The ^{14}C uptake experiments and the calculation of primary production as well as Chl *a* measurement were described in the same paper. Briefly, water samples for ^{14}C uptake experiments and Chl *a* were taken from depths based on light penetration (usually 100, 55, 30, 10, 3, and 1% of surface irradiance). The incubation period for ^{14}C uptake was 4 h. The daily primary productivity in the water column was calculated based on the ratio of irradiance during the incubation to the daily total irradiance and integrated through the six sample depths. Chl *a* was measured onboard ship and integrated through the same sample depths.

T–S diagrams and entrainment of NO_3

Temperature and salinity (T–S) diagrams were used to indicate the entrainment process and to calculate the amount of entrained NO_3, as described in Yin et al. (1995*a*). The method is briefly described here. A vertical profile of temperature and salinity at one station generates a T–S diagram. All T–S diagrams along the transect from the same day were plotted in one graph and they formed a triangular envelope due to colder temperature of the freshwater in the river. The three water types were then determined: freshwater, estuarine plume water, and deep seawater. The data points of salinity and temperature (S, T) of freshwater and the deep seawater were obtained from the in situ measurements (two points of the triangle) and the third data point of the estuarine plume was estimated based on all the T–S curves of the graph. The shape of the triangle changed from day to day, since 1 day of T–S diagrams produced one graph. Thus, the data points (S, T) of the estuarine plume changed daily and the problem of temperature change caused by daily surface heating was minimized. The proportion of each water type was calculated and used to calculate the contribution of each water type to the NO_3 concentrations present in the water column. At some depth, the freshwater proportion was zero. By integrating NO_3 in the upper layer above this depth, the amount of NO_3 minus freshwater-borne NO_3 from the river was the amount of entrained NO_3. More details are given in Yin et al. (1995*a*). In this calculation, the amount of entrained NO_3 was a minimum estimate, since biological uptake was not included.

Data on tides, winds, and river discharge

Observed hourly tidal heights were provided by the Tides and Current Section, Institute of Ocean Sciences, Sidney, B.C., Canada. The discharge data for the Fraser River at Hope were obtained from the Water Survey of Canada. The wind data were recorded at the Vancouver International Airport and provided by the Atmospheric Service, Environment Canada.

Results

During the cruise between June 12 and 19, 1991, the Fraser River discharge was 6250 $m^3 \cdot s^{-1}$ on June 12. Then it increased rapidly, reached a peak (7500 $m^3 \cdot s^{-1}$) on June 15, close to the annual maximum (8010 $m^3 \cdot s^{-1}$) that occurred on July 3, 1991, and then decreased afterwards (Fig. 2). There was a spring tide that lasted for almost 3 days between June 12 and 14 and the following neap tide occurred on June 19. Daily averaged wind speeds were 2–5 $m \cdot s^{-1}$ (Fig. 2).

Phytoplankton biomass and production

Chl *a* concentrations ranged from about 10 to 50 $mg \cdot m^{-2}$, but on June 18, Chl *a* reached over 100 $mg \cdot m^{-2}$ at P5 and about 75 $mg \cdot m^{-2}$ at P7 and S1 (Fig. 3). Primary production ranged from almost zero at S2 on June 15 to over 4000 mg $C \cdot m^{-2} \cdot d^{-1}$ at P5 on June 18. The Chl *a* concentrations and primary

Fig. 2. Daily averaged river discharge, wind speed, and tidal ranges during the cruise (June 12–19). The annual river discharge for 1991 at Hope is included.

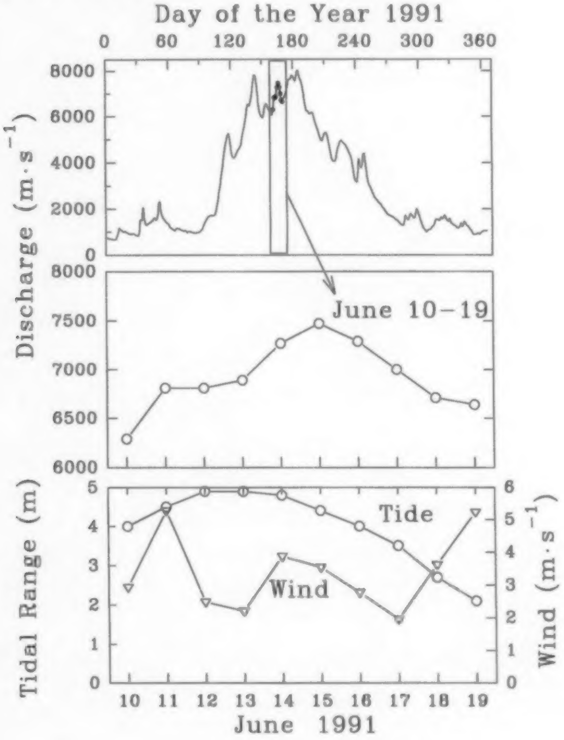
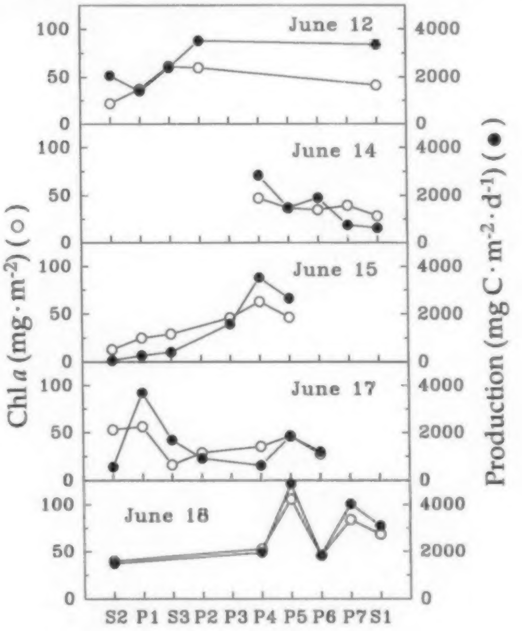


Fig. 3. Spatial distribution of Chl *a* and primary production along the transect (see Fig. 1) during June 12–18.



production were usually lower near the river mouth, except for June 17, and higher at intermediate stations along the transect (e.g., P4 during June 14–15; Fig. 3).

Fluorescence

A subsurface fluorescence maximum was present at all the stations on June 12 and at the seaward stations (P4, P5, and S1) on June 15, but it disappeared at S3 and was eroded at the seaward stations (P4, P5, and S1) on June 17 (Fig. 4). On June 19, the fluorescence maximum occurred near the surface and increased in thickness.

Hydrography

The surface salinity increased seaward from S3 to S1 but decreased over time at P5 and S1, particularly during June 15–17, 1991 (Fig. 5), indicating a seaward expansion of the freshwater influence as well as a downward penetration of freshwater. This increase in thickness and size of the estuarine plume reflected the peak in river discharge that occurred on June 15. An important feature in the salinity structure was that there was no clear upper mixed layer because the salinity increased stepwise with depth down to 20 m except at S3 on June 19. This characteristic is further demonstrated in T–S diagrams (Fig. 6).

The T–S curves were approximately bent into two parts. The break point usually occurred between salinities of 25 and 27, with a twist in some curves (e.g., P4 on June 15 and P5 on June 17) (Fig. 6). The left part of the T–S curve represented the estuarine plume including the main halocline and the right part represented the deep water below. In particular, the left parts on June 17 were flattened, reflecting colder upper layer temperatures on June 17 than on June 15.

River discharge mainly causes horizontal flow shears that result in entrainment. A T–S diagram can serve as a good indicator of these mixing processes. A change in the slope of the T–S diagram can indicate which process has been dominant. In the Strait of Georgia, heating mainly determines the T–S slope before the annual freshet in river discharge, which starts in April. Once the river discharge increases rapidly, the T–S slope of a recent mixture of freshwater and seawater will be bent horizontally from the previous slope. As shown in Fig. 6, the slopes for the right part of the T–S curves are parallel to one another and steeper than the left part, indicating that the lower layer was formed before the annual freshet. The slopes for the left parts of the T–S curves indicate that freshwater input was dominant over heating in shaping the structure of the water column. The break point between the left part and the right part in the T–S diagram is important in quantifying entrained NO_3.

Nutrients

The transient nature of the hydrodynamics affects the distribution of nutrients. On June 12, NO_3 was undetectable at the surface and the nutricline was below 8 m at S3 and 12 m at P5 and S1 (Fig. 7). On June 15, at the seaward stations of P5 to S1, the NO_3 distribution remained similar whereas at S3, NO_3 concentrations at the surface increased due to the riverine plume invasion and the nutricline rose (Fig. 7). The concentration of NO_3 was about 20 µM at 20 m, except at P4. On June 17, the nutricline moved upwards and became broader at

Fig. 4. Vertical profiles of fluorescence along the transect (see Fig. 1) during June 12–19.

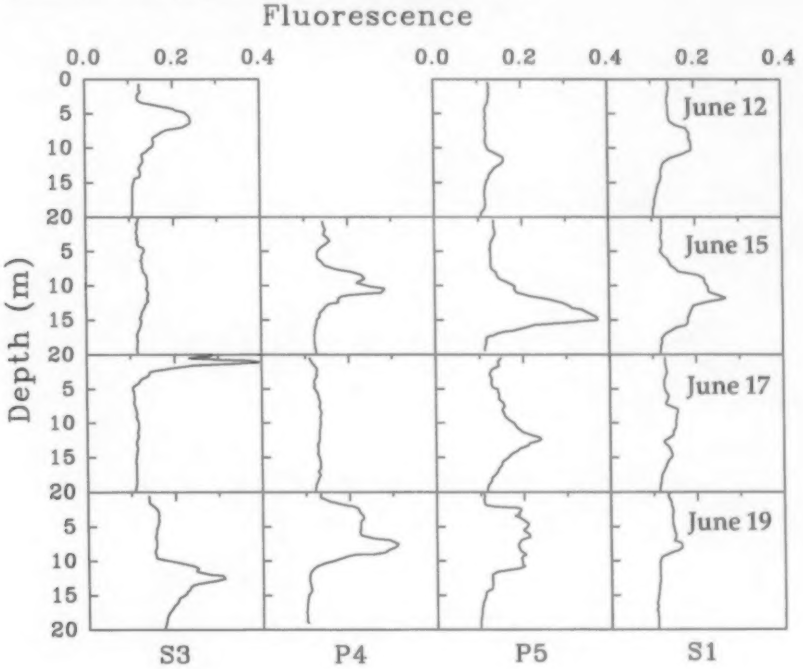
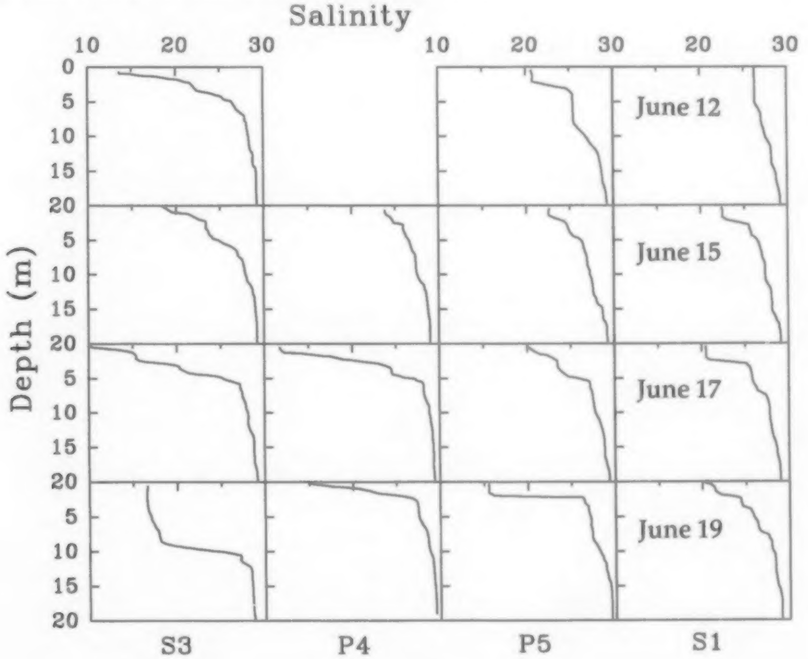


Fig. 5. Vertical profiles of salinity along the transect (see Fig. 1) during June 12–19.



P4 to S1, which indicates that NO_3 concentrations increased in the top 10 m of the water column. However, the increase was at the expense of a decrease in NO_3 concentrations in the lower layer where the NO_3 concentration was about 15 μM at 20 m. By June 19, NO_3 concentrations decreased in the top 10 m, particularly at S3 and P4.

The distribution of SiO_4 was a good tracer for the coupling between the salinity and NO_3 distributions. Because SiO_4 in

Fig. 6. Vertical profiles of temperature and salinity (T–S diagrams) along the transect (see Fig. 1) during June 12–19.

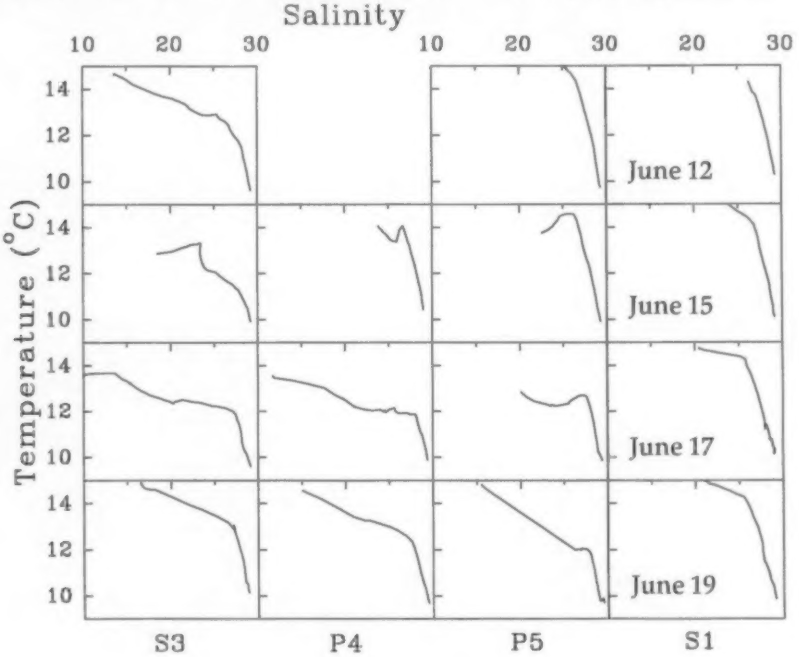
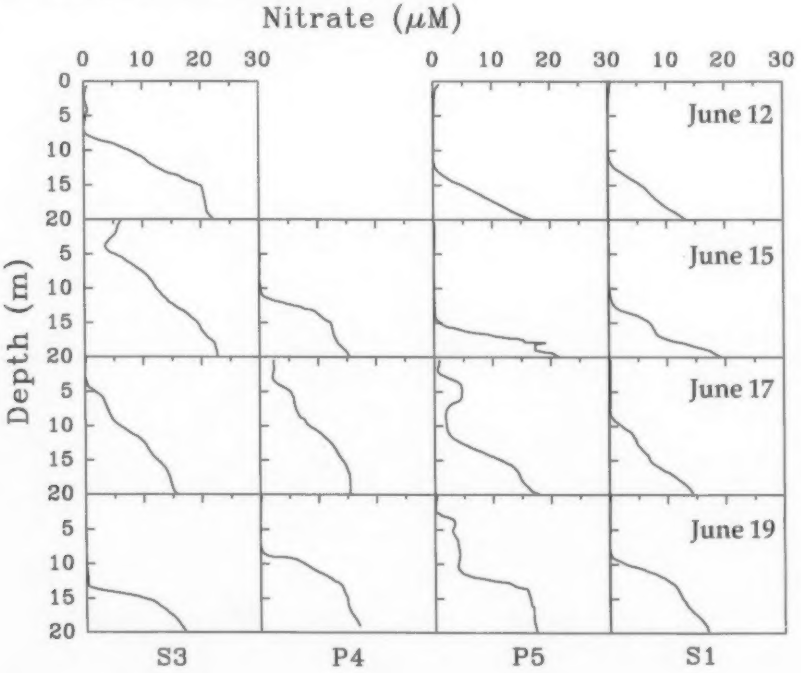
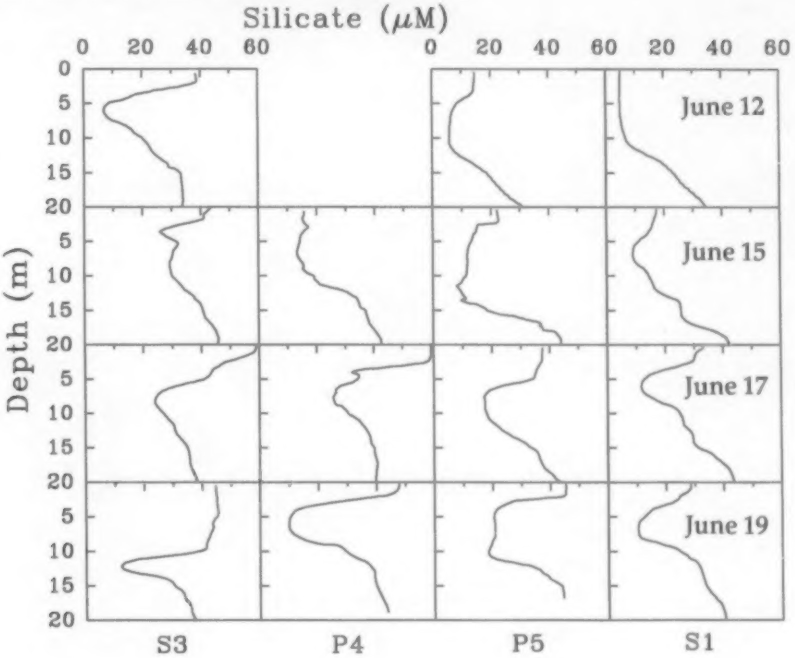


Fig. 7. Vertical profiles of NO_3 along the transect (see Fig. 1) during June 12–19.



the river was usually much higher (approximately 82 μM) than in both the surface water of the estuarine plume and the seawater at depth (20 m), its distribution (Fig. 8) reflected horizontal advection and vertical mixing of the riverine plume and estuarine plume as well as biological consumption. On June 12, SiO_4 at the surface decreased seaward, being very low at S1,

Fig. 8. Vertical profiles of SiO_4 along the transect (see Fig. 1) during June 12–19.



higher at P5, and reaching 40 μM at S3. A subsurface minimum in SiO_4 concentration was formed at intermediate depths (5–11 m) between S3 and P5. The higher surface SiO_4 reflected the recent outflow of freshwater and the minimum indicated biological utilization in the estuarine plume before the riverine plume covered it. On June 15 when the near-maximum river discharge occurred, SiO_4 concentrations at the surface increased greatly (Fig. 8). On June 17, SiO_4 concentrations further increased at both the surface and the subsurface SiO_4 minimum at all the stations except S3. By June 19, SiO_4 concentrations at the surface and at the subsurface minimum decreased (Fig. 8).

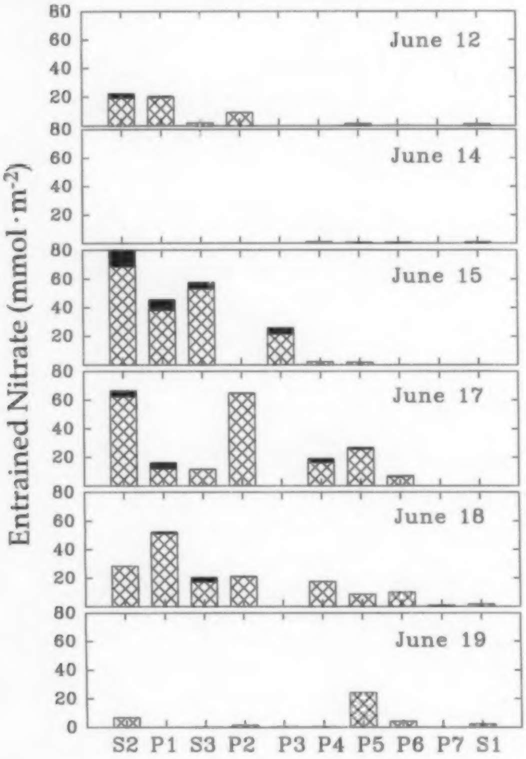
Entrainment of NO_3

The rapid increase in river discharge from June 11 to 15 (Fig. 2) resulted in the expansion of the area and thickness of the estuarine plume with a time lag, as shown in the vertical profiles of salinity (Fig. 5). As a result of the movement of the estuarine plume, there was entrainment of NO_3 from the deep NO_3-rich seawater into the estuarine plume as indicated in both the T–S diagrams and the profiles of NO_3. For example, the drop in temperature at the twist (e.g., P5 on June 17) indicated colder deep water that was high in NO_3, and correspondingly, there was a subsurface NO_3 maximum (Fig. 7). The upward movement of the nutricline on June 17 also indicated entrainment of NO_3.

One of the difficulties in estimating the amount of entrained NO_3 is to determine a depth above which NO_3 is considered to be entrained and available for biological uptake. In this system, the water column could be divided into an upper and a lower layer. The upper layer was not homogeneously mixed during periods of high river discharge because of the tide-modulated river outflow. When freshwater was discharged, it would be mixed by winds from the surface and by tides from the bottom as it moved away, and thus, new freshwater was added to the water column before a mixed layer was formed. Such a feature is shown as stepwise increases with depth in the salinity structure (Fig. 5). This upper layer is represented by the left part of a T–S curve. In contrast, the lower layer was relatively well mixed and could be defined by the water mass represented by the right part in a T–S diagram. The amount of NO_3 in the upper layer was considered to be that which was entrained.

There were temporal and spatial changes in the amount of entrained NO_3 (Fig. 9). During June 12–14, there was little entrained NO_3 and little river-borne NO_3. On June 15, a massive amount of NO_3 (from 40 to 80 $mmol \cdot m^{-2}$) at S2–S3 was entrained at the stations near the river mouth as the amount of river-borne NO_3 increased. This was a response to a maximum river discharge occurring on this day, which was consistent with our previous study (Yin et al. 1995*b*). During June 17–18, entrainment of NO_3 increased at the seaward stations. This suggests that either the entrained NO_3 near the river mouth moved seawards, or the response to the maximum river discharge at those stations lagged that at the stations near the river mouth, or a combination of both. By June 19, the amount of entrained NO_3 was largely reduced, indicating subsequent utilization of the entrained NO_3 as the river discharge decreased. The utilization of NO_3 resulted in an increase in fluorescence at intermediate depths (Fig. 4). In spite of the increased river discharge during the cruise, river-borne NO_3 remained only a small portion of NO_3 in the water column along the transect. The amount of entrained NO_3 was 5–10 times more than that of river-borne NO_3.

Fig. 9. Estimate of entrained NO_3 along the transect during the cruise (June 12–19). The solid black portion on the top of the bar is the amount of river-borne NO_3. The concentration of NO_3 in the Fraser River freshwater was 5.3 μM during this period.



Discussion

The rapid increase in river discharge was clearly responsible for the increased entrainment of NO_3 observed during June 15–17. Winds and the tidal cycles could not be responsible for the observed entrainment of NO_3 during June 15–17. It is known that a spring tide and strong winds induce more entrainment than a neap tide and weak winds (Yin et al. 1995*b*, 1995*c*). The tidal cycles during June 14–17 were in transition from the end of the spring tide to the beginning of the neap tide. More entrainment of nutrients should have been observed on June 11 than on June 17, if only the tidal cycle was the dominant force in entrainment. Winds were weak (<4 m·s^{-1}) during the same period. Even though wind speed was twice as strong on June 11 as on June 12, the features of the entrainment of NO_3 that occurred on June 17 were not observed on June 12. It is possible that on June 11, biological uptake of NO_3 balanced the horizontal and vertical input of NO_3 by wind and tidal mixing. Thus, the trace of vertical mixing of NO_3 might not be seen in the profiles on June 12. High primary production at P2 and S1 on June 12 could have resulted from the stronger winds on June 11.

In 1990, a similar response to a fluctuation in river discharge was observed during a cruise between May 29 and June 7. NO_3 concentrations increased in the surface layer at the same stations as in this study, reaching almost 10 μM at some stations on June 3 (Clifford et al. 1991), when the Fraser River discharge rate rapidly increased from 7000 to almost 10 000 m^3·s^{-1} from May 29 to June 3. Winds were weak during the same period and could not have accounted for the increase in NO_3 concentration.

As a result of nutrient entrainment, phytoplankton biomass and primary productivity in this study were comparable with values during the spring bloom in early April for the same year (Yin et al. 1996) and were higher than those values reported by Parsons et al. (1969) for the same region. Similarly, phytoplankton biomass and primary productivity in June 1990 were at comparable levels at four stations along the same transect as in this study. Particularly on June 2, primary productivity reached 5.8 g C·m^{-2}·d^{-1} at P5, which was comparable with the highest values reported by Stockner et al. (1979). These high levels of phytoplankton biomass and primary productivity indicated that entrainment of nutrients due to the maximal river discharge produced a major bloom. It is known that the Strait of Georgia is a highly productive region, comparable with other eutrophied estuaries. Nutrients in the Fraser River were previously perceived as a major reason for this high productivity (Stockner et al. 1979). Later, entrainment of nutrients was proposed to be responsible for the nutrient supply (Parsons et al. 1980); however, there has been no direct evidence for the central Strait before this study. This observation demonstrates that the central Strait can be productive during the maximum river discharge in late May and June even when nutrients in the Fraser River are low during the same period.

Entrainment induced by a fluctuation in river discharge was superimposed on the maximum river discharge. There are implications for other estuaries. Discharge in rivers varies seasonally. It is well known that river outflow controls the dynamics of nutrients and primary production on a seasonal and annual basis (e.g., St. Lawrence estuary (Therriault and Levasseur 1986), Chesapeake Bay (Fisher et al. 1988; Malone et al. 1988), and San Francisco Bay (Cloern et al. 1983)). These studies demonstrate that the seasonal change in river discharge often leads to spatial progression of the seasonal bloom along the estuaries. However, discharge in the river also fluctuates daily or weekly such as in the Fraser River and St. Lawrence River as well as the Columbia River due to increased snowmelt during sunny weather. There are no studies on the effects of a fluctuation on such short time scales. Presumably, entrainment results in a dilution with seawater when nutrients in freshwater are higher than in its adjacent seawater. An increase or decrease in river discharge over a short time scale would result in corresponding temporal and spatial variations in the distribution of nutrients and phytoplankton biomass along an estuary. Downstream of the estuary where nutrients are depleted in the surface layer, such a fluctuation might be an important driving force in entrainment of nutrients between the surface nutrient-depleted layer and the deep nutrient-rich layer. In estuaries where nutrients in the river are lower than in its adjacent seawater, entrainment induced by the fluctuation in river discharge would be an important mechanism for supplying nutrients to the euphotic zone. For example, the Amazon River, the largest river in the world, belongs to this type of estuary. A region of high biological activity in the Guiana Current between the coast of the Guianas and the lens of freshened surface water was reported to be due to entrainment (Ryther et al. 1967). The entrainment of NO_3 was observed in the Amazon plume (Edmond et al. 1981; Muller-Karger et al. 1988).

In conclusion, the results of this study demonstrate that the structure of water properties such as salinity, temperature, nutrients, and fluorescence in the central Strait responds rapidly to changes in river discharge. These findings confirm that entrainment of nutrients into the estuarine plume is due to the outflow of the Fraser River discharge and entrainment provides nutrients to the euphotic zone and maintains relatively high primary production in May and June, well after the spring bloom in March–April. The dynamics of nutrients and primary productivity also responded to a fluctuation in river discharge superimposed on the seasonal change. The entrainment of NO_3 during the peak of the freshet was 5–10 times more important than river-borne NO_3. The timing and magnitude of the May–June freshet could significantly influence primary productivity during this period. Through this mechanism of nutrient entrainment into the photic zone, high production of the higher trophic levels including fish can be supported in the Strait of Georgia.

Acknowledgements

We would like to thank Dr. Mike St. John, who coordinated the cruises, and Peter Clifford, who conducted ^{14}C uptake experiments and other measurements. Thanks are extended to the Department of Fisheries and Oceans for providing ship time and the officers and crew of C.S.S. *Vector* for their assistance. This research was funded by a Natural Sciences and Engineering Research Council of Canada (NSERC) strategic grant. The Research Fellowship to support Kedong Yin was kindly provided by the Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C., Canada.

References

Armstrong, F.A.J., Stearns, C.R., and Strickland, J.D.H. 1967. The measurement of upwelling and subsequent biological processes by means of the Technicon AutoAnalyzer and associated equipment. Deep-Sea Res. **14**: 381–389.

Bailey, G.W., and Chapman, P. 1991. Short-term variability during an anchor station study in the southern Benguela upwelling system: chemical and physical oceanography. Prog. Oceanogr. **28**: 9–37.

Clifford, P.J., Harrison, P.J., Yin, K., St. John, M.A., Waite, A.M., and Albright, L.J. 1990. Plankton production and nutrient dynamics in the Fraser River plume, 1988. Manuscr. Rep. No. 53. Department of Oceanography, University of British Columbia, Vancouver, B.C.

Clifford, P.J., Harrison, P.J., Yin, K., St. John, M.A., and Goldblatt, R. 1991. Plankton production and nutrient dynamics in the Fraser River plume, 1990. Manuscr. Rep. No. 58. Department of Oceanography, University of British Columbia, Vancouver, B.C.

Cloern, J.E., Alpine, A.E., Cole, B.E., Wong, R.L.J., Arthur, J.F., and Ball, M.D. 1983. River discharge controls phytoplankton dynamics in the Northern San Francisco Bay Estuary. Estuarine Coastal Shelf Sci. **16**: 415–429.

Cordes, R.E., Pond, S., de Lange Boom, B.R., LeBlond, P.H., and Crean, P.B. 1980. Estimates of entrainment in the Fraser River plume, British Columbia. Atmosphere–Ocean, **18**: 15–26.

Edmond, J.M., Boyle, E.A., Grant, B., and Stallard, R.F. 1981. The chemical mass balance in the Amazon plume I: the nutrients. Deep-Sea Res. **28**: 1339–1374.

Fisher, T.R., Harding, L.W. Jr., Stanley, D.W., and Ward, L.G. 1988. Phytoplankton, nutrients and turbidity in the Chesapeake, Delaware and Hudson estuaries. Estuarine Coastal Shelf Sci. **27**: 61–93.

Greisman, P., and Ingram, G. 1977. Nutrient distribution in the St. Lawrence Estuary. J. Fish. Res. Board Can. **34**: 2117–2123.

Hager, S.W., Gordon, L.I., and Park, P.K. 1968. A practical manual for the use of Technicon AutoAnalyzer in seawater nutrient analysis. A Final Report to B.C.F., contract 14-17-0001-1759, October 1968, Reference 68-73.

Harrison, P.J., Fulton, J.D., Taylor, F.J.R., and Parsons, T.R. 1983. Review of the biological oceanography of the Strait of Georgia: pelagic environment. Can. J. Fish. Aquat. Sci. **40**: 1064–1094.

Harrison, P.J., Clifford, P.J., Cochlan, W.P., Yin, K., St. John, M.A., Thompson, P.A., Sibbald, M.J., and Albright, L.J. 1991. Nutrient and phytoplankton dynamics in the Fraser River plume, Strait of Georgia, British Columbia. Mar. Ecol. Prog. Ser. **70**: 291–304.

Ingram, R.G. 1979. Water masses modification in the St. Lawrence Estuary. Nat. Can. **106**: 45–54.

Jones, D.M., Harrison, P.J., Clifford, P.J., Yin, K., and St. John, M.A. 1991. A computer-based system for the acquisition and display of continuous vertical profiles of temperature, salinity, fluorescence and nutrients. Water Res. **25**: 1545–1548.

LeBlond, P.H. 1983. The Strait of Georgia: functional anatomy of a coastal sea. Can. J. Fish. Aquat. Sci. **40**: 1033–1063.

Malone, T.C., Crocker, L.H., Pike, S.E., and Wendler, B.W. 1988. Influences of river flow on the dynamics of phytoplankton production in a partially stratified estuary. Mar. Ecol. Prog. Ser. **48**: 235–249.

Mann, K.H., and Lazier, J.R.N. 1991. Dynamics of marine ecosystems: biological–physical interactions in the oceans. Blackwell Scientific Publications, Inc., Cambridge, Mass.

Muller-Karger, F.E., McClain, C.R., and Richardson, P.L. 1988. The dispersal of the Amazon's water. Nature (Lond.), **333**: 56–58.

Norcross, J.J., and Stanley, E.M. 1967. Inferred surface and bottom drift, June 1963 through October 1964. Circulation of shelf waters off the Chesapeake Bight. Prof. Pap. Environ. Sci. Serv. Admin. **3**: 11–42.

Pape, E.H., and Garvine, R.W. 1982. The subtidal circulation in Delaware Bay and adjacent shelf waters. J. Geophys. Res. **87**: 7955–7970.

Parsons, T.R., Stephens, K., and LeBrasseur, R.J. 1969. Production studies in the Strait of Georgia. Part 1. Primary production under the Fraser River plume, February to May, 1967. J. Exp. Mar. Biol. Ecol. **3**: 27–38.

Parsons, T.R., LeBrasseur, R.J., and Barraclough, W.E. 1970. Levels of production in the pelagic environment of the Strait of Georgia, British Columbia: a review. J. Fish. Res. Board Can. **27**: 1251–1264.

Parsons, T.R., Albright, L.J., and Parslow, J. 1980. Is the Strait of Georgia becoming more eutrophic? Can. J. Fish. Aquat. Sci. **37**: 1043–1047.

Pitcher, G.C., Walker, D.R., Mitchell-Innes, B.A., and Moloney, C.L. 1991. Short-term variability during an anchor station study in the southern Benguela upwelling system: phytoplankton dynamics. Prog. Oceanogr. **28**: 9–37.

Pond, S., and Pickard, G.L. 1978. Introductory dynamic oceanography. Pergamon Press, Toronto, Ont.

Ryther, J.D., Menzel, D.W., and Corwin, N. 1967. Influence of the Amazon River outflow on the ecology of the western tropical Atlantic. I. Hydrography and nutrient chemistry. J. Mar. Res. **25**: 69–83.

Sinclair, M., El-Sabh, M.I., and Brindle, J.-R. 1976. Seaward nutrient transport in the lower St. Lawrence estuary. J. Fish. Res. Board Can. **33**: 1271–1277.

Slawyk, G., and MacIsaac, J.J. 1972. Comparison of two automated ammonium methods in a region of coastal upwelling. Deep-Sea Res. **19**: 521–524.

Steven, D.M. 1974. Primary and secondary production in the Gulf of St. Lawrence. McGill Univ. Mar. Sci. Cent. Manuscr. Rep. No. 26.

Stockner, J.G., Cliff, D.D., and Shortreed, K.R.S. 1979. Phytoplankton ecology of the Strait of Georgia, British Columbia. J. Fish. Res. Board Can. **36**: 657–666.

Therriault, J.-C., and Lacroix, G. 1976. Nutrients, chlorophyll, and internal tides in the St. Lawrence Estuary. J. Fish. Res. Board Can. **33**: 2747–2757.

Therriault, J.-C., and Levasseur, M. 1986. Freshwater runoff control of the spatio-temporal distribution of phytoplankton in the lower St. Lawrence estuary. *In* The role of freshwater outflow in coastal marine ecosystems. *Edited by* S. Skreslet. NATO ASI Ser. Vol. G7. Springer-Verlag, Berlin. pp. 251–260.

Waldichuk, M. 1957. Physical oceanography of the Strait of Georgia, British Columbia. J. Fish. Res. Board Can. **14**: 321–486.

Wood, E.D., Armstrong, F.A.J., and Richards, F.A. 1967. Determination of nitrate in seawater by cadmium–copper reduction to nitrite. J. Mar. Biol. Assoc. U.K. **47**: 23–31.

Yin, K., Harrison, P.J., Pond, S., and Beamish, R.J. 1995*a*. Entrainment of nitrate in the Fraser River plume and its biological implications. I. Effects of salt wedge. Estuarine Coastal Shelf Sci. **40**: 505–528.

Yin, K., Harrison, P.J., Pond, S., and Beamish, R.J. 1995*b*. Entrainment of nitrate in the Fraser River plume and its biological implications. II. Effects of spring vs neap tides and river discharge. Estuarine Coastal Shelf Sci. **40**: 529–544.

Yin, K., Harrison, P.J., Pond, S., and Beamish, R.J. 1995*c*. Entrainment of nitrate in the Fraser River plume and its biological implications. III. Effects of winds. Estuarine Coastal Shelf Sci. **40**: 545–558.

Yin, K., Harrison, P.J., Goldblatt, R.H., and Beamish, R.J. 1996. Spring bloom in the central Strait of Georgia: interactions of river discharge, winds and grazing. Mar. Ecol. Prog. Ser. **138**: 255–263.

Relationships between body mass, population density, and the self-thinning rule in stream-living salmonids

Jason B. Dunham and Gary L. Vinyard

Abstract: In food and (or) space-limited populations, increases in average body size may be accompanied by increases in per capita space and (or) energy requirements. Thus, as body size increases in time or space, the equilibrium number of individuals that can be supported in a given environment should decrease. This relationship, referred to as self-thinning, produces a negative linear relationship between log body size (mass) and log population density. We studied body mass – population density relationships in stream-living populations of several trout species from the intermountain western United States. Our analyses of relationships between body mass and population density demonstrated that self-thinning can be manifested through both temporal and spatial variability in fish population characteristics. Several populations did not show self-thinning, possibly due to species-specific traits, temporal and spatial environmental variation, or both. Thinning lines may not reveal specific causal mechanisms, but they appear to be real, density-dependent responses and thus offer a potentially useful method for studying fish populations. Experimental studies of self-thinning under more controlled conditions are needed, however, to identify causal mechanisms and eliminate alternative explanations for body size – abundance relationships.

Résumé : Dans les populations limitées par la nourriture et (ou) l'espace, les augmentations de la taille corporelle moyenne peuvent s'accompagner d'une augmentation des besoins en espace et (ou) en énergie par individu. Ainsi, au fur et à mesure que la taille corporelle augmente dans le temps et dans l'espace, le nombre d'individus qu'un environnement donné peut soutenir en équilibre devrait diminuer. Cette relation d'autodécroissance produit une relation linéaire négative entre le log de la taille corporelle (masse) et le log de la densité de la population. Nous avons étudié les relations masse corporelle-densité de population chez des populations de plusieurs espèces de truites de ruisseau dans l'ouest des États-Unis (*intermountain western United States*). Nos analyses des relations entre la masse corporelle et la densité de population ont montré que l'autodécroissance peut se manifester aussi bien par suite de la variabilité temporelle que spatiale des caractéristiques de la population de poissons. Plusieurs populations n'ont pas fait preuve d'autodécroissance, peut-être à cause de caractéristiques spécifiques de l'espèce, d'une variation environnementale spatiale et temporelle, ou des deux. Les lignes d'autodécroissance peuvent ne pas révéler les mécanismes causaux spécifiques, mais elles semblent être réelles et, de ce fait, constituent une méthode potentiellement utile pour étudier les populations de poissons. Toutefois, des études expérimentales de l'autodécroissance dans des conditions mieux contrôlées sont nécessaires pour déterminer les mécanismes causaux et éliminer les autres explications pour les relations taille corporelle-abondance.
[Traduit par la Rédaction]

Introduction

Individual variation in body size has important implications for population structure and dynamics (Peters 1983; Werner and Gilliam 1984; omnicki 1988). In fishes, body size is related to a variety of ecologically important characteristics, including competitive ability, survivorship, fecundity, diet breadth, and growth rate (Wootton 1990). Because larger individuals generally require more resources, the equilibrium number of individuals supported in a given environment (carrying capacity) should depend on average body size. The expected relationship between equilibrium population density (N) and average body size (mass, W) is commonly expressed as

$$(1) \quad N = aW^{-b}$$

where a and b are constants referring to the intercept and slope, respectively, of the body mass – population density regression. When this pattern is observed within species, it is referred to as self-thinning, a result of intraspecific competition for limited resources. Self-thinning has been studied extensively in plants, but only recently has attention been directed at mobile animal populations (Begon et al. 1986; Fréchette and Lefaivre 1995).

Some of the best evidence for self-thinning in fish populations comes from studies of stream-living salmonids in northwest England (Elliott 1993; Grant 1993), southern Sweden (Bohlin et al. 1994), and experimental stream channels (Grant 1993). The existence of a self-thinning relationship implies that some factor or combination of factors is acting to limit population density. Two factors, space and food, are thought to be of primary importance in limiting salmonid production

Received February 27, 1996. Accepted October 7, 1996.
J13322

J.B. Dunham.[1] Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, NV 89557, U.S.A.
G.L. Vinyard. Program in Ecology, Evolution and Conservation Biology and Department of Biology, University of Nevada, Reno, NV 89557, U.S.A.

[1] Author to whom all correspondence should be addressed.

in streams (Chapman 1966). Thinning lines (eq. 1) for stream-living salmonids limited by space (territoriality) are predicted to have a slope of approximately –0.93 (Grant and Kramer 1990; Grant 1993), while lines for food-limited populations are predicted to have a slope of approximately –0.88 (Bohlin et al. 1994). The territory size thinning line is an empirical estimate derived from the relationship between territory size and body mass (Grant and Kramer 1990; Grant 1993), while the food limitation line is based on the theoretical concept of "energetic equivalence" (Damuth 1981; Nee et al. 1991; Bohlin et al. 1994). Because (as we show in this study) slopes of thinning lines predicted from food and space limitation are very similar, they may be difficult to distinguish in practice.

Energetic equivalence is based on the fact that per capita energetic requirements increase as body mass increases. This increase is not 1:1, however, because metabolic rate slows down as body mass increases. The relationship between body mass and metabolic rate is

$$(2) \qquad M = aW^b$$

where M is metabolic rate (milligrams O_2 per hour) and a and b are regression parameter estimates (Glass 1969). According to the energetic equivalence hypothesis, slopes of relationships between population density and average body mass should be the inverse of slopes relating metabolic rate and body mass ($-b$, see Bohlin et al. 1994 for further discussion). If this holds, the sum of individual energy requirements remains constant during self-thinning (=energetic equivalence). In other words, total energy flow through a population is independent of population density. This is expected if fish populations are limited by constant energy (food) inputs.

Slopes of thinning lines in stream-living salmonid populations studied to date generally are consistent with the energetic equivalence prediction (Elliott 1993; Grant 1993; Bohlin et al. 1994); thus, it appears that food, rather than space limitation, is more common (but see Keeley and Grant 1995). In this paper, we further investigate evidence for energetic equivalence in stream-living salmonids and attempt to identify important factors that may explain empirical deviations from its predictions.

Data used in this study come from intensive surveys of Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) populations in Great Basin (United States) streams and from long-term population surveys of resident trout throughout the intermountain region of the western United States (Platts and Nelson 1988). We studied relationships between body mass and population density to (*i*) look for the existence of thinning lines in these data sets, (*ii*) examine the evidence for food and (or) space limitation, and (*iii*) examine spatial and temporal variation in self-thinning. To explicitly test for independence of energy flow through a population and population density, we compared a regression model of population energy flow based on average body mass with an individual-based method.

Materials and methods

Study sites

Study areas for long-term population surveys are described in Platts and Nelson (1988). Field surveys of Lahontan cutthroat trout were conducted during the summers of 1993–1994 in tributaries of the upper Humboldt River, Humboldt and Elko counties, Nevada. Streams ranged in elevation from 1700 to 2300 m. Average water depths in the study areas were generally 15 cm or less, while wetted stream channel widths averaged 1–4 m. Stream conditions in this region are highly variable in space and time (Platts and Nelson 1988; Nelson et al. 1992). Winter conditions are often severe, with cold temperatures, anchor ice, and avalanches at higher elevations. In some years, heavy spring runoff leads to severe flooding, which may directly kill or displace fishes (Seegrist and Gard 1972; Erman et al. 1988; Strange et al. 1992). Summer air temperatures often exceed 30°C, with daily water temperature fluctuations of up to 20°C. Drought conditions in 1994 led to extensive stream drying and fish mortality in areas just downstream of several study sites (J.B. Dunham and G.L. Vinyard, personal observation). Other fish species, including Tahoe sucker (*Catostomus tahoensis*), speckled dace (*Rhinichthys osculus*), and Piute sculpin (*Cottus beldingi*), occurred in the study streams, but Lahontan cutthroat trout were generally the numerically dominant fish species present.

Sampling methods

In both data sets (long-term and Lahontan cutthroat trout), fish populations were sampled by electrofishing and population estimates obtained from multiple-pass depletions (van Deventer and Platts 1989). Details of sampling methods for long-term surveys are given in Platts and Nelson (1988). We used survey data from Platts and Nelson (1988) that spanned at least 5 yr with areal biomass estimates consistently greater than $0.1\ g \cdot m^{-2}$.

Lahontan cutthroat trout data came from surveys of abundance at 42 sites in six streams in 1993 and at 49 sites in seven streams in 1994 ($n = 7$ sites per stream). Sites without fish were dropped from the analysis. When possible, the same sites were sampled in each year. Each site consisted of an approximately 25-m stream reach blocked at up- and downstream ends with fine-mesh (3- to 4-mm-diameter) seines to prevent fish escape during sampling. As with the long-term data (Platts and Nelson 1988), fish population density was expressed as number per unit area. Population estimates were obtained separately for young-of-year (age 0) and older (age 1+) fish. All sampling was conducted during summer base-flow conditions (late July – September).

Statistical analyses

Body mass – abundance regressions

We analyzed body mass – abundance using ordinary least squares and reduced major axis (RMA, McArdle 1988) regression with population density (N) as the response and average body size (W) as a predictor variable with categorical stream effects in the model (Myers 1990). Abundance data from Platts and Nelson (1988) included several salmonid species (bull trout (*Salvelinus confluentus*), brook trout (*S. fontinalis*), Lahontan cutthroat trout (*Oncorhynchus clarki*), rainbow trout (*O. mykiss*), and brown trout (*Salmo trutta*)) in several streams. Stream and species effects could not be distinguished, so data were analyzed with a combined species–stream categorical variable to simultaneously account for species and stream effects. Data were analyzed with the SAS General Linear Models procedure (Littell et al. 1991). Data were $\log_{10}$ transformed to linearize the relationship

$$\log(N) = \log(a) - b\log(W)$$

with terms as defined above.

The first step in the analysis was to ensure that model assumptions were satisfied. Residuals were obtained from the linearized statistical model and examined for normality with the SAS Univariate procedure (Littell et al. 1991). Output indicated that studentized residuals were normally distributed, but a Levene's test (Kuehl 1994) on the absolute residuals indicated significant variance heterogeneity in the Lahontan cutthroat trout data. Because the models tested here are based on log–log relationships between body size and abundance, we

Table 1. Analysis of variance table for multiple regression analysis of the long-term data set ($R^2 = 0.90$).

Source	df	MS	*F*	*P*
Species stream	8	0.167	4.69	0.0003
Average body mass	1	0.775	21.78	0.0001
Interaction	8	0.824	2.89	0.0109
Error	45	0.036		

did not attempt further transformations. Instead, a weighted analysis was conducted by using $1/\sigma_i^2$ for body size at the *j*th site in stream *i*, following recommendations in Myers (1990) and Littell et al. (1991). This was necessary for both body size – abundance analyses and analyses of energy flow in relation to population density for Lahontan cutthroat trout (see Population energy flow below).

A preliminary analysis indicated (species–stream)·body size interactions were significant ($P < 0.05$) in the long-term data set, so slopes and intercepts were determined separately for each population. Stream·body size interactions were not significant ($P > 0.20$) for the Lahontan cutthroat trout data, so the interaction term was dropped and the analysis was run again to estimate slopes.

Population energy flow

According to the hypothesis of energetic equivalence, population energy flow should be independent of population density. Thus far, theoretical arguments about relationships between body size and population density have been based on the relationship between *average* body mass and abundance. If the distribution of body sizes has a large variance or is substantially skewed, then average body size may poorly represent total energy flow in a population or community (Cyr and Pace 1993). If there is no size variation among individuals, overall energy flow through a population, *F*, is represented as

$$(3) \qquad F = aW^b \cdot N,$$

the product of average mass-specific energy requirements (aW^b) and population density (fish per square metre). If, however, there is substantial variation in the distribution of body sizes, then overall energy flow through a population is more correctly specified as the sum of individual energy requirements. Taking *w* as individual body mass and summing for $i = 1$ to *n*, the number of individuals in a population, total energy flow may be calculated as follows:

$$(4) \qquad F = aw^b \cdot \mathrm{m}^{-2}.$$

This formulation is more realistic for populations with large variation or skewed distribution in body size, as is often the case for species with Type III survivorship (e.g., fishes). Note in this case that total energy flow (*F*) is expressed in units of milligrams O_2 per hour per square metre, which may be converted to energetic equivalents (Elliott and Davison 1975).

To compare the influence of underlying size frequency distributions on the relationship between body size and population density, we compared regressions of estimated total energy flow calculated from averages and from individuals versus population density. Total energy flow based on average and individual body mass was estimated as described above and analyzed in relation to population density using the log-transformed linear model. Total energy flow was estimated using constants for *O. nerka*, obtained by Brett (1965). Differences between actual numbers of fish captured and population estimates (van Deventer and Platts 1989) were generally very small (<10%). In cases where population estimates exceeded the number of fish captured, energy flow based on individuals was calculated by substituting average body size in place of the uncaptured individuals at each site. Average body size was calculated separately for young-of-year (age 0) and older (age 1+) fish and multiplied by the number of uncaptured individuals in the corresponding size class to estimate total energy flow.

Results

Body size – abundance

For the long-term data set, multiple regression with body mass and the composite species–stream categorical variable explained approximately 90% of the variance in population density (Table 1). The moderately strong interaction between body mass and species–stream indicates that the slope of the relationship between body size and abundance depends on stream effects, species effects, or a combination of both. For the 1993 Lahontan cutthroat trout data, multiple regression indicated a weak, but significant stream·body size interaction effect ($F = 2.96, P < 0.03, \mathrm{df} = 5$) and significant stream effects ($F = 7.17, P < 0.0003, \mathrm{df} = 5$), but no significant effect of body size alone (overall model $R^2 = 0.87$). Body size was highly significant for the 1994 Lahontan cutthroat trout data ($F = 40.79, P < 0.0001, \mathrm{df} = 1$), with significant stream effects as well ($F = 15.62, P < 0.0001, \mathrm{df} = 5$), but no significant stream·body size interaction (i.e., among-stream differences in regression slopes could not be distinguished). Together, body size and stream effects explained 80% of the variance in population density in 1994 ($R^2 = 0.81$).

Of the nine species–stream ordinary least squares slope estimates (b_{OLS}) in the long-term data (Fig. 1), four were found to be statistically significant (Table 2). With the exception of the RMA slope estimate (b_{RMA}) for bull trout, 95% confidence intervals around *b* included values predicted by the energetic equivalence and territory limitation hypotheses. The ordinary least squares slope of the body size – abundance regression for Lahontan cutthroat trout surveyed in 1994 was -0.99 ± 0.26 (95% CI), while the RMA slope estimate was -1.10, with the 95% CI ranging from -1.12 to -0.90. The latter slope estimate is significantly steeper than slope predictions from food limitation (-0.88), but not different from the slope predicted by space limitation (-0.93).

Energy flow versus population density

Self-thinning generally did not apply for Lahontan cutthroat trout sampled in 1993 (Fig. 2). As a consequence, we only considered data from 1994. Multiple regression with stream effects included in the model as above indicated no significant relationships between population density and energy flow estimated from averages and individuals for Lahontan cutthroat trout sampled in 1994. Probability (*P*) values from partial *F*-tests of population density effects were 0.81 and 0.15 for energy flow estimated from averages and individuals, respectively.

Discussion

Results from this study are more equivocal than previous investigations of self-thinning in stream-living salmonids (Grant and Kramer 1990; Elliott 1993; Grant 1993; Bohlin et al. 1994). Below, we discuss possible reasons for differences between our results and those from previous studies and briefly discuss what we view as important and untested issues and assumptions that must be addressed before self-thinning is widely accepted as a real phenomenon.

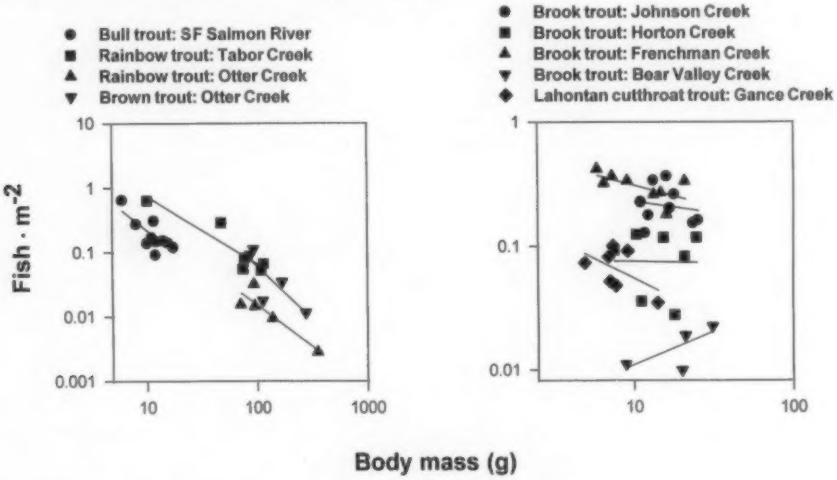


Fig. 1. Scatterplots of body mass – population density relationships for five salmonid species studied in nine streams (data from Platts and Nelson 1988). Each point represents one annual population estimate. Thinning lines with significant slopes (Table 2) are shown in the left graph, while those with nonsignificant slopes are shown in the right graph.

Table 2. Parameter estimates and 95% CI for slopes from regression analyses of body size versus abundance in the long-term data set (Platts and Nelson 1988).

Species (locality)	b_{RMA} (95% CI)	b_{OLS} (±95% CI)	n	P
Bull trout	−1.79	−1.40	11	0.0033
(SF Salmon River)	(−2.81, −1.13)	(±1.02)		
Rainbow trout	−1.14	−1.06	6	0.0001
(Tabor Creek)	(−1.91, −0.69)	(±0.60)		
Rainbow trout	−1.43	−1.28	5	0.0006
(Otter Creek)	(−3.01, −0.68)	(±1.17)		
Brown trout	−2.06	−1.65	5	0.0007
(Otter Creek)	(−5.37, −0.80)	(±1.43)		
Brook trout	—	−0.19	9	NS
(Johnson Creek)	—	(±1.23)		
Brook trout	—	−0.02	7	NS
(Horton Creek)	—	(±1.09)		
Brook trout	—	−0.34	8	NS
(Frenchman Creek)	—	(±0.86)		
Brook trout	—	0.54	5	NS
(Bear Valley Creek)	—	(±1.51)		
Cutthroat trout	—	−0.65	8	NS
(Gance Creek)	—	(±1.36)		

Note: Sample sizes (n) represent the number of annual surveys. P-values are for slopes (b_{OLS}). RMA slopes (b_{RMA}) were not estimated when least squares were not significant (McArdle 1988).

Evidence for self-thinning

Combined evidence from this study and others (Elliott 1993; Grant 1993; Bohlin et al. 1994) suggests that self-thinning may occur in stream-living salmonids, but exceptions here require further explanation. In the long-term data set, several species–stream combinations did not show a significant self-thinning pattern (Table 2). Regression slopes for streams with bull, rainbow, and brown trout all showed the pattern expected from self-thinning, while streams with Lahontan cutthroat trout and brook trout did not. The consistent lack of a self-thinning pattern for brook trout is especially noticeable, with 5–9 yr of data from four different streams showing no relationship between average body mass and population density. If there are indeed species-specific differences in body size – abundance relationships, perhaps these can be attributed to different habitat preferences and competitive interactions (Gard 1961; Rodríguez 1995). Alternatively, stream habitats in this study may not have supported brook trout populations at equilibrium density.

Abundance and energy flow

Our finding of no significant relationship between population density and energy flow estimated from averages or individuals suggests that the use of averages in body size – abundance regressions did not bias our analyses supporting energetic equivalence for Lahontan cutthroat trout in 1994. In other words, food limitation appears to be operating to adjust population density in relation to per capita energy requirements such that energy flow remains constant. This assumes, of course, that food limitation is directly operating to limit populations (see Defining causal mechanisms below).

There are ecological as well as statistical reasons for considering the underlying distribution of body sizes in body size – abundance analyses. Bohlin et al. (1994) correctly pointed out that ontogenetic changes in diet, mortality, and growth may lead to b-values substantially different from those predicted by the hypothesis of energetic equivalence. Our data sets cover a relatively wide range of body sizes within and among streams, but overall homogeneity of slopes for streams with wide variation in body size in the 1994 Lahontan cutthroat trout data suggests that b-values are similar in this range.

Results from other studies of stream-living salmonids indicate that ontogenetic dietary differences may not be as large as one might suspect. A recent study of dietary overlap in stream-living Colorado cutthroat trout (*Oncorhynchus clarki pleuriticus*, Bozek et al. 1994) found considerable overlap in taxonomic composition and size of food items consumed by individuals ranging from 24 to 188 mm (total length) and that food items too large to be accommodated by the gape size of age 0 fish were rarely encountered. Mortality patterns also may not vary substantially for different size classes because all populations in this study were surveyed during low summer flows. Summer mortality in stream-living salmonids is generally low in comparison with winter and spring (Seegrist and Gard 1972; Strange et al. 1992; Hutchings 1993). However, during our studies of Lahontan cutthroat trout, large adults occasionally were observed acting aggressively toward smaller individuals. Thus, smaller individuals may be displaced to areas of higher predation risk and reduced growth.

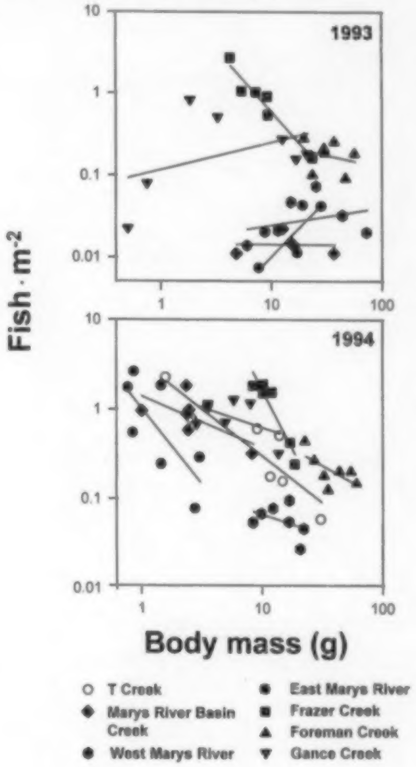
Temporal versus spatial variation

Confidence intervals for slopes and intercepts are much wider for the long-term data (Platts and Nelson 1988) than for the Lahontan cutthroat trout data set. Since the former data were from annual surveys and the latter were from surveys conducted in a single year, increased variability in the long-term data may reflect higher temporal variation in ecological factors affecting salmonid populations. The contrasting results for self-thinning in Lahontan cutthroat trout in 1993 and 1994 lead us to suspect that environmental variation has a large temporal component. This also may explain why body mass – abundance regressions for Lahontan cutthroat trout were not significant in the long-term data. For this reason, we suggest that parameter estimates for body mass – abundance regressions will be more precise when population data come from many sites sampled in a relatively narrow time period, as opposed to fewer sites sampled over longer (e.g., yearly) time periods.

Strong temporal effects on body mass – abundance relationships are suggested by our data that show a strong self-thinning pattern for Lahontan cutthroat trout in 1994, but not in 1993. The significant stream·body size interaction observed in 1993 was probably due to the strong, negative relationship between body mass and population density in Frazer Creek (Fig. 2). Other streams sampled in 1993 give little indication of such a relationship (Fig. 2).

We suspect that differences between these two years are related to variation in stream discharge. Data collected by the U.S. Geological Survey in the upper Humboldt River basin, Nevada (which includes Gance Creek), show that stream discharges in 1994 were among the lowest recorded in the last 50 yr. Low water levels and reduced habitat volume may have caused an intraspecific competitive "crunch" (sensu Wiens 1977) during drought conditions of 1994.

Fig. 2. Scatterplots of body mass – population density relationships for Lahontan cutthroat trout studied in six streams in 1993 and seven streams in 1994 (T Creek added in 1994). Each point represents a population estimate for one site. Regression lines are the weighted least squares line for each population.



Defining causal mechanisms

When populations in this study did show patterns expected with self-thinning, slopes of thinning lines were equally compatible with predictions from food (energetic equivalence) or space (territoriality) limitation. Two exceptions were bull trout in the long-term data, where the b_{RMA} slope was steeper than either slope predicted by space or food limitation, and the Lahontan cutthroat trout data for 1994, where the b_{RMA} slope was consistent with space limitation, but significantly steeper than predicted by food limitation. Analyses of energy flow in relation to population density for Lahontan cutthroat trout in 1994 are consistent with food limitation, however. Our inability to distinguish between space and food limitation may stem from several related complications in the analysis of thinning lines. First, predicted slopes from the food and space limitation hypotheses are very similar (approximately –0.88 versus –0.93, respectively), so random error in estimates of body size and population density must be very small to effectively distinguish alternatives. Natural variability in environmental conditions also may increase variation around thinning lines, possibly affecting slopes and intercepts as well. It is well known that temperature and metabolic rate are closely coupled in fishes. For example, metabolic scaling exponents (b in eq. 2) for brown trout were found to range from 0.92 to 1.15, depending on temperature (Beamish 1964; Glass 1969). Predicted slopes of thinning lines for food-limited brown trout populations thus range similarly as ambient temperatures vary. Other factors such as spatial and (or) temporal variation in underwater visibility, habitat structure, or physicochemical conditions may also affect behavioral interactions and metabolic rates. Finally, a recent analysis of this problem by Marschall and Crowder (1995) suggests that food and space limitation may be theoretically indistinguishable.

In closing, we must mention our concerns with the use of observational data and correlational analyses to examine thinning lines. In this study, we considered only body mass as a correlate of population density. Significant correlations between these variables may not be a direct result of causal relationships.

This could be a problem for at least two important reasons. First, we have no direct, independent measure of food and (or) space limitation. Second, body mass may be affected by factors with little relation to intraspecific competition for food and (or) space, such as size-related predation risk or proximity to spawning areas (e.g., Beard and Carline 1991). Before self-thinning becomes a widely accepted phenomenon, we emphasize the need for experimental studies under more controlled conditions (e.g., Begon et al. 1986; Latto 1994; Fréchette and Lefaivre 1995) to more clearly define causal mechanisms.

Acknowledgements

We thank P. Coffin, G. Johnson, D. Lee, J. McIntyre, R. Nelson, and especially B. Rieman for their suggestions during the formative stages of this research. B. Rieman, J. Hayes, S. Jenkins, M. Reed, and two anonymous reviewers provided constructive improvements to earlier drafts of the manuscript. G. Fernandez provided valuable statistical advice. Special thanks to S. Dunham, T. Jenni, P. Fischer, and M. Olsen for field assistance. Major funding for this work was provided by a grant from the USDA Forest Service Intermountain Research Station to G. Vinyard (INT-92731-RJVA). Additional support was provided by the Biological Resources Research Center and Biology Department, University of Nevada–Reno. This work would not have been possible without permission of Region I U.S. Fish and Wildlife Service and the Nevada Department of Wildlife (permit Nos. S-9039, S-0153, and S-12357).

References

Beamish, F.W.H. 1964. Respiration of fishes with special emphasis on standard oxygen consumption. II. Influence of weight and temperature on respiration of several species. Can. J. Zool. **42**: 177–188.

Beard, T.D., Jr., and Carline, R.F. 1991. Influence of spawning and other stream habitat features on the spatial variability of wild brown trout. Trans. Am. Fish. Soc. **120**: 711–722.

Begon, M., Firbank, L., and Wall, R. 1986. Is there a self-thinning rule for animals? Oikos, **46**: 122–124.

Bohlin, T., Dellefors, C., Faremo, U., and Johlander, A. 1994. The energetic equivalence hypothesis and the relation between population density and body size in stream-living salmonids. Am. Nat. **143**: 478–493.

Bozek, M.A., Debray, L.D., and Lockwood, J.A. 1994. Diet overlap among size classes of Colorado river cutthroat trout (*Oncorhynchus clarki pleuriticus*) in a high-elevation mountain stream. Hydrobiologia, **273**: 9–17.

Brett, J.R. 1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. **22**: 1491–1501.

Chapman, D.W. 1966. Food and space as regulators of salmonid populations in streams. Am. Nat. **100**: 345–357.

Cyr, H., and Pace, M.L. 1993. Allometric theory: extrapolations from individuals to communities. Ecology, **74**: 1234–1245.

Damuth, J. 1981. Population density and body size in mammals. Nature (Lond.), **290**: 699–700.

Elliott, J.M. 1993. The self-thinning rule applied to juvenile sea-trout, *Salmo trutta*. J. Anim. Ecol. **62**: 371–379.

Elliott, J.M., and Davison, W. 1975. Energy equivalents of oxygen consumption in animal energetics. Oecologia, **19**: 195–201.

Erman, D.C., Andrews, E.D., and Yoder-Williams, M. 1988. Effects of winter floods on fishes in the Sierra Nevada. Can. J. Fish. Aquat. Sci. **45**: 2195–2200.

Fréchette, M., and Lefaivre, D. 1995. On self-thinning in animals. Oikos, **73**: 425–428.

Gard, R. 1961. Effects of beaver on trout in Sagehen creek, California. J. Wildl. Manage. **25**: 221–242.

Glass, N.R. 1969. Discussion of calculation of power function with special reference to respiratory metabolism in fish. J. Fish. Res. Board Can. **26**: 2643–2650.

Grant, J.W.A. 1993. Self-thinning in stream-dwelling salmonids. *In* Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. *Edited by* R.J. Gibson and R.E. Cutting. Can. Spec. Publ. Fish. Aquat. Sci. No. 118. pp. 99–102.

Grant, J.W.A., and Kramer, D.L. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Can. J. Fish. Aquat. Sci. **47**: 1724–1737.

Hutchings, J.A. 1993. Adaptive life histories effected by age-specific survival and growth rate. Ecology, **74**: 673–684.

Keeley, E.R., and Grant, J.W.A. 1995. Allometric and environmental correlates of territory size in juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **52**: 186–196.

Kuehl, R.O. 1994. Statistical principles of research design and analysis. Duxbury Press, Belmont, Calif.

Latto, J. 1994. Evidence for a self-thinning rule in animals. Oikos, **69**: 531–534.

Littell, R.C., Freund, R.J., and Spector, P.C. 1991. SAS system for linear models. SAS Institute Inc., Cary, N.C.

Łomnicki, A. 1988. Population ecology of individuals. Princeton University Press, Princeton, N.J.

Marschall, E.A., and Crowder, L.B. 1995. Density-dependent survival as a function of size in salmonids in streams. Can. J. Fish. Aquat. Sci. **52**: 136–140.

McArdle, B.H. 1988. The structural relationship: regression in biology. Can. J. Zool. **66**: 2329–2339.

Myers, R.H. 1990. Classical and modern regression with applications. 2nd ed. Duxbury Press, Belmont, Calif.

Nee, S., Read, A.F., Greenwood, J.J.D., and Harvey, P.H. 1991. The relationship between body size and abundance in British birds. Nature (Lond.), **351**: 312–313.

Nelson, R.L., Platts, W.S., Larsen, D.P., and Jensen, S.E. 1992. Trout distribution and habitat in relation to geology and geomorphology in the North Fork Humboldt River drainage, northeastern Nevada. Trans. Am. Fish. Soc. **121**: 405–426.

Peters, R.H. 1983. Ecological implications of body size. Cambridge University Press, New York.

Platts, W.S., and Nelson, R.L. 1988. Fluctuations in trout populations and their implications for land-use evaluation. N. Am. J. Fish. Manage. **8**: 333–345.

Rodríguez, M.A. 1995. Habitat-specific estimates of competition in stream salmonids: a field test of the isodar model of habitat selection. Evol. Ecol. **9**: 169–184.

Seegrist, D.W., and Gard, R. 1972. Effects of floods on trout in Sagehen Creek, California. Trans. Am. Fish. Soc. **102**: 478–482.

Strange, E.L., Moyle, P.B., and Foin, T.D. 1992. Interactions between stochastic and deterministic processes in stream fish community assembly. Environ. Biol. Fishes, **36**: 1–15.

van Deventer, J.S., and Platts, W.S. 1989. Microcomputer software system for generating population statistics from electrofishing data — user's guide for microfish 3.0. USDA Gen. Tech. Rep. INT-254.

Werner, E.E., and Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. **15**: 393–425.

Wiens, J.A. 1977. On competition in variable environments. Am. Sci. **65**: 590–597.

Wootton, R.J. 1990. Ecology of teleost fishes. Chapman and Hall, New York.

An examination of the PCB:lipid relationship among individual fish

Craig A. Stow, Leland J. Jackson, and James F. Amrhein

Abstract: We examined data from 1984 to 1994 for five species of Lake Michigan salmonids to explore the relationship between total PCB concentration and percent lipid. When we compared mean species lipid and PCB values, we found a strong linear correlation. When we compared values among individuals, we found modest positive PCB:lipid associations in brown trout (*Salmo trutta*), chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), and rainbow trout (*Oncorhynchus mykiss*) collected during spawning, but positive associations were not apparent among nonspawning individuals. Lake trout (*Salvelinus namaycush*) exhibited no discernible PCB:lipid relationship. Our results are not incompatible with previous observations that contaminants are differentially partitioned into lipids within a fish, but these results do suggest that lipids are not a major factor influencing contaminant uptake.

Résumé : Nous avons examiné les données de 1984 à 1994 sur cinq espèces de salmonidés du lac Michigan pour étudier la relation entre la concentration totale de BPC et le pourcentage de lipides. Lorsque nous avons comparé les valeurs moyennes de lipides et de BPC dans les espèces, nous avons trouvé une forte corrélation linéaire. Lorsque nous avons comparé les valeurs entre les individus, nous avons décelé des relations BPC : lipides faiblement positives chez la truite brune (*Salmo trutta*), le saumon chinook (*Oncorhynchus tshawytscha*), le saumon coho (*Oncorhynchus kisutch*) et la truite arc-en ciel (*Oncorhynchus mykiss*) capturés pendant le frai, mais il n'y avait pas de relation positive apparente chez les sujets qui ne frayent pas. Le touladi (*Salvelinus namaycush*) ne présentait pas de relation BPC : lipides discernable. Nos résultats ne sont pas incompatibles avec des observations antérieures selon lesquelles les contaminants sont répartis différemment dans les lipides chez les poissons, mais ces résultats indiquent que les lipides ne constituent pas un facteur important influant sur l'absorption des contaminants.

[Traduit par la Rédaction]

Introduction

It is a virtual paradigm that contaminants and lipids in fishes are strongly linked. This idea arose early in the study of fish contaminant biology and appears to be rooted in the observation that fattier portions of fishes contain higher concentrations of organochlorine contaminants (Reinert 1969). Early research also revealed that contaminant differences between fish species were correlated with average species lipid concentrations (Reinert 1970). Hamelink et al. (1971) proposed that the elevated contaminant levels observed in fishes were due to an exchange equilibrium between water and fat such that lipophilic contaminants differentially partitioned into fatty tissue. In the approximately 25 yr since these early developments, a large body of literature has accumulated supporting, and building on, the general idea that lipid concentration is largely responsible for organochlorine contaminant bioaccumulation.

An ensuing debate has also occurred during this time, regarding the primary mechanism of bioaccumulation. Two alternative schools of thought have arisen. One school advocates bioconcentration, the diffusive uptake of contaminants directly from the aqueous environment, to be responsible for elevated biotic contaminant levels (Leblanc 1995). The competing school supports the idea of biomagnification, a successive increase in contaminants with each ascending food web tier, resulting from eating contaminated prey in lower tiers, as the dominant bioaccumulation mechanism (Rasmussen et al. 1990). Lipid partitioning is fundamental to both schools and detailed mechanistic models have been developed demonstrating the feasibility of both direct uptake (e.g., Barber et al. 1991) and food chain accumulation (e.g., Gobas et al. 1993) based on the lipophilic tendencies of organochlorine contaminants.

It is noteworthy that there is minimal published empirical scrutiny of the relationship between fish lipid content and organochlorine contaminant levels. If lipids strongly influence contaminant uptake, either by direct uptake or by contaminated prey consumption, we would expect that individual fish would exhibit strong correlations between organochlorine and lipid concentrations. However, most analyses that identify the importance of lipids have been based on a highly aggregate comparison of different species of fish or fish from different locations (Rasmussen et al. 1990; Rowan and Rasmussen 1992; Ewald and Larsson 1994) or they have examined the compartmentalization of contaminants and lipids within fish (Niimi and Oliver 1983, 1989; Voiland et al. 1991).

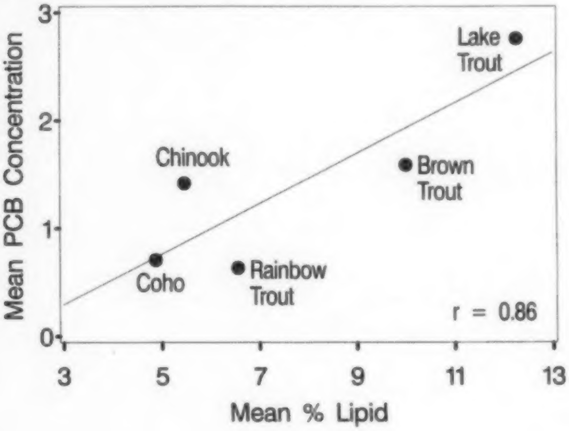
More recently, Larsson et al. (1996) examined Atlantic salmon (*Salmo salar*) from the Baltic Sea and found total PCBs, and other organic contaminants, to be positively related to percent lipid in muscle tissue of spawning individuals. This result appears to contrast another recent analysis of individual

Received March 29, 1996. Accepted October 7, 1996.
J13379

C.A. Stow.[1] Nicholas School of the Environment, Duke University, Box 90328, Durham, NC 27708-0328, U.S.A.
L.J. Jackson. Department of Natural Resources and Environmental Sciences, University of Illinois, 1102 South Goodwin Avenue, Urbana, IL 61801, U.S.A.
J.F. Amrhein. Wisconsin Department of Natural Resources, Madison, WI 53706, U.S.A.

[1] Author to whom all correspondence should be addressed. e-mail: cstow@duke.edu

Fig. 1. Sample mean PCB concentration versus sample mean % lipid for brown trout ($n = 220$), chinook salmon ($n = 452$), coho salmon ($n = 269$), lake trout ($n = 396$), and rainbow trout ($n = 220$).



fish (Stow 1995) that indicated no residual PCB:lipid relationship among five species of Lake Michigan fishes, after the PCB concentration data were adjusted for size, location, species, and year-to-year variation.

In this analysis, we further examine the relationship between total PCB concentration and lipid content among individual fish in a considerably expanded data set ($n = 1557$) of five species of Lake Michigan salmonids: brown trout (*Salmo trutta*), chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), lake trout (*Salvelinus namaycush*), and rainbow trout (*Oncorhynchus mykiss*). We selected data from 1984 to 1994 representing a period when PCB concentrations showed no appreciable trends (Stow 1995) and collection and analytical protocols were consistent. Our analysis indicates modest positive PCB:lipid relationships in brown trout, chinook salmon, coho salmon, and rainbow trout collected during spawning, but not among nonspawning individuals. Lake trout exhibit no discernible PCB:lipid relationship, and there is a suggestion of a slight negative PCB:lipid relationship among nonspawning rainbow trout. These results imply that a positive PCB:lipid relationship may be related to changes in fish tissue occurring during spawning and cast further doubt on bioconcentration as an important uptake mechanism.

Materials and methods

Analytical methods

The data were collected and analyzed by the Michigan and Wisconsin Departments of Natural Resources. All analyses were done using skin-on fillets. Collected fish were filleted, wrapped in aluminum foil, and transported on ice to a facility where they were frozen until analysis. Michigan DNR samples were analyzed in accordance with either established Food and Drug Administration (1977) protocol or Michigan Department of Public Health methods (Price et al. 1986). All Wisconsin Department of Natural Resources samples were analyzed at the Wisconsin State Laboratory of Hygiene. A detailed description of the analytical protocol is presented in Stow et al. (1994). Lipid analysis was performed following the same sample cleanup and extraction procedures cited above. A 2-mL aliquot of the extract was transferred to an aluminum weighing dish. The solvent was evaporated under a stream of air and the residue was weighed to the nearest 0.1 mg. Final separation and quantitation of all samples was done using electron-capture gas chromatography.

Statistical methods

Data were analyzed using the general linear models procedure in SAS software (SAS Institute Inc. 1987). To determine the presence of a statistically discernible lipid effect, log-transformed total PCB data were regressed on log-transformed length and lipid data, with location and year also included as categorical predictor variables for each species. Standard assumptions regarding independence and homogeneity of the disturbance term variance were corroborated by viewing residual plots. We prepared added variable plots (partial residual plots) by regressing log PCB on all of the predictor variables except log lipid, then regressing log lipid on these same predictor variables, and graphing the residuals from the two regressions as a bivariate plot (Weisberg 1985). These plots provide a depiction of the PCB:lipid relationship remaining after both PCB and lipid have been adjusted for the effects of length, location, and year.

Results

A positive association between sample mean species PCB and lipid concentrations is readily discernible in these data (Fig. 1). However, species plots of PCB concentration versus lipid for individual fish reveal only weakly perceptible patterns (Fig. 2) and sample correlations that are all less than 0.13. The PCB:lipid relationship for chinook is negative, with a correlation of –0.13.

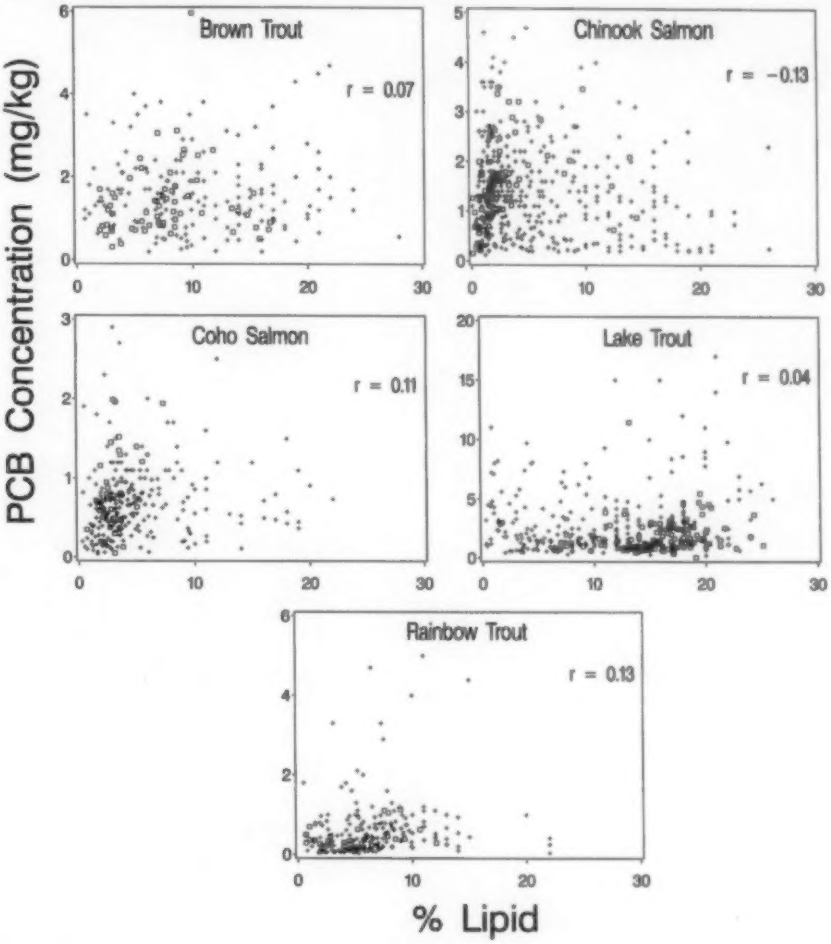
A relationship between PCB concentration and fish size exists for four of five species (Fig. 3) with sample correlations for these four species ranging from 0.34 to 0.63. The pattern is particularly pronounced for lake trout, with individuals above 60 cm showing relatively large PCB increases. The PCB:size relationship is visible, even though these data represent fish collected from many sites over an 11-yr period. A PCB:size relationship is not visibly apparent for rainbow trout, possibly because of the mix of sampling locations. Eight of the nine visible outliers for rainbow trout under 40 cm are from the Sheboygan River, an area with heavy PCB contamination. If all Sheboygan River data are excluded, the PCB:size correlation for rainbow trout increases to 0.25 ($n = 196$).

Lipid concentration is also somewhat related to size for all five species (Fig. 4). These relationships are slight but sufficient to be confounding when separating associations with PCB concentration. As they did with the PCB:lipid relationship, chinook salmon display a negative lipid:size correlation, unlike the other four species.

We performed regression analyses on these data, with various combinations of the predictor and response variables in the natural and log metrics, with differing degrees of spatial aggregation in the location variable, and with varying levels of interaction among the predictor variables. The qualitative results did not change. The only notable exception was that length appeared as a statistically discernible factor for rainbow trout in the log metric but not in the natural metric.

Regression results indicate a discernible PCB:lipid relationship in chinook and coho salmon and brown trout, but not in lake or rainbow trout (Table 1). Prompted by the results of Larsson et al. (1996), we further explored this relationship by dividing all five species into two groups: individuals collected during September and October, when many fish sampled are in spawning condition, and nonspawning individuals. Analysis of only nonspawning individuals indicates none of the five

Fig. 2. Total PCB concentration versus % lipid for each of the five salmonid species. Symbols indicate Wisconsin Department of Natural Resources data (pluses) and Michigan Department of Natural Resources data (squares).



species exhibits a statistically discernible PCB:lipid relationship. However, individuals collected during spawning exhibit a discernible relationship in all species except lake trout. Added variable plots (Fig. 5) provide a visualization of the PCB:lipid relationship in spawning and nonspawning fish, and the partial correlations are a measure of the strength of this relationship. Brown trout, chinook and coho salmon, and rainbow trout all exhibit a positive, albeit noisy relationship among spawning individuals. Lake trout display no relationship in either nonspawning or spawning individuals.

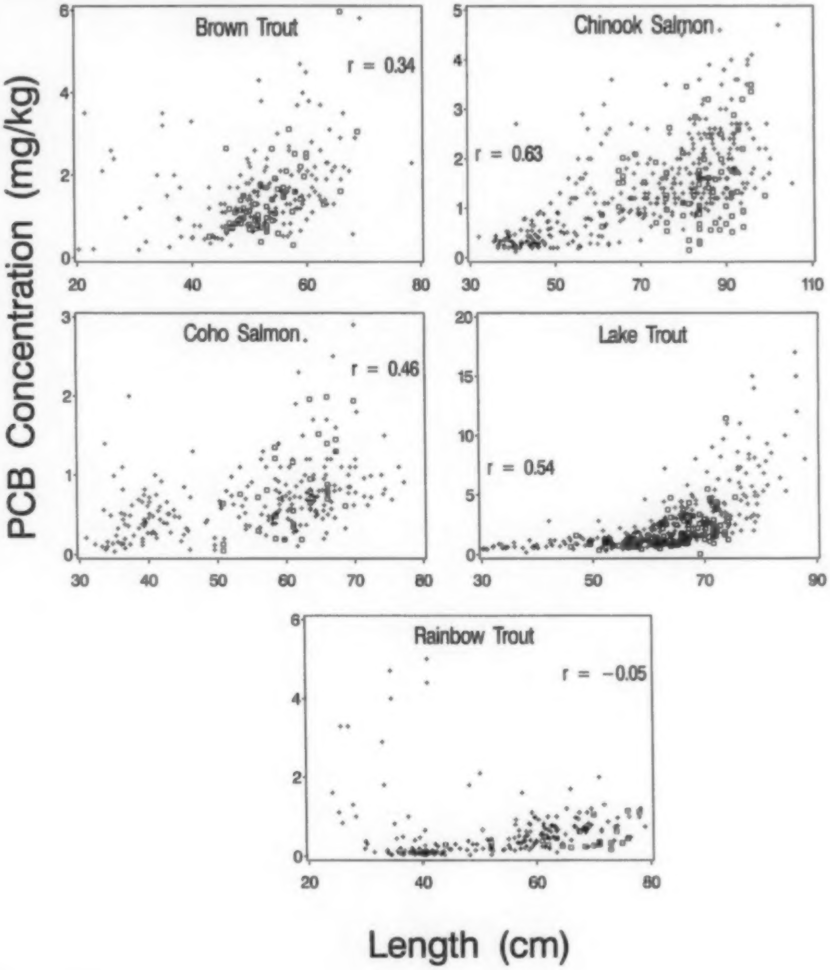
We note that the raw data plots (Fig. 2) indicate a negative PCB:lipid as well as a negative lipid:size relationship (Fig. 4) for chinook salmon. The adjusted data reveal a positive PCB:lipid relationship for chinook, indicating that the negative relationship in the raw data is primarily due to the confounding effect of size.

Discussion

A cursory analysis of these data, based on a comparison of sample means (Fig. 1), appears consistent with currently accepted ideas regarding the importance of lipids in contaminant bioaccumulation. However, analyses of individual fish indicate that the relationship is less clear. The observation that lake trout exhibit no PCB:lipid relationship and only individuals collected during spawning display a relationship in the other four species appears inconsistent with current ideas regarding mechanisms of lipophilic contaminant bioaccumulation. Yet, this observation is not inconsistent with the repeated observation that contaminants are differentially deposited in fatty tissue (Reinert 1969; Reinert et al. 1972; Skea et al. 1979). Possibly, within an individual, contaminants accumulate in lipid, but lipid concentration may be unimportant in the mechanism governing contaminant assimilation.

Differential contaminant accumulation in lipid could also be responsible for differences between spawning and nonspawning individuals. As fish enter spawning condition, energy reserves are mobilized into gonad production and spent in migration. Additionally, a portion of the contaminant burden is transferred to eggs (Miller 1993). Conceivably, a concurrent

Fig. 3. Total PCB concentration versus length for each of the five salmonid species. Symbols indicate Wisconsin Department of Natural Resources data (pluses) and Michigan Department of Natural Resources data (squares).



reduction in lipid-stored energy and organochlorine contaminants could induce a perceptible PCB:lipid association in fish in spawning condition. The absence of a perceptible association in lake trout could occur because both PCB and lipid concentrations are more variable than in other species and a higher variance obfuscates patterns induced by spawning.

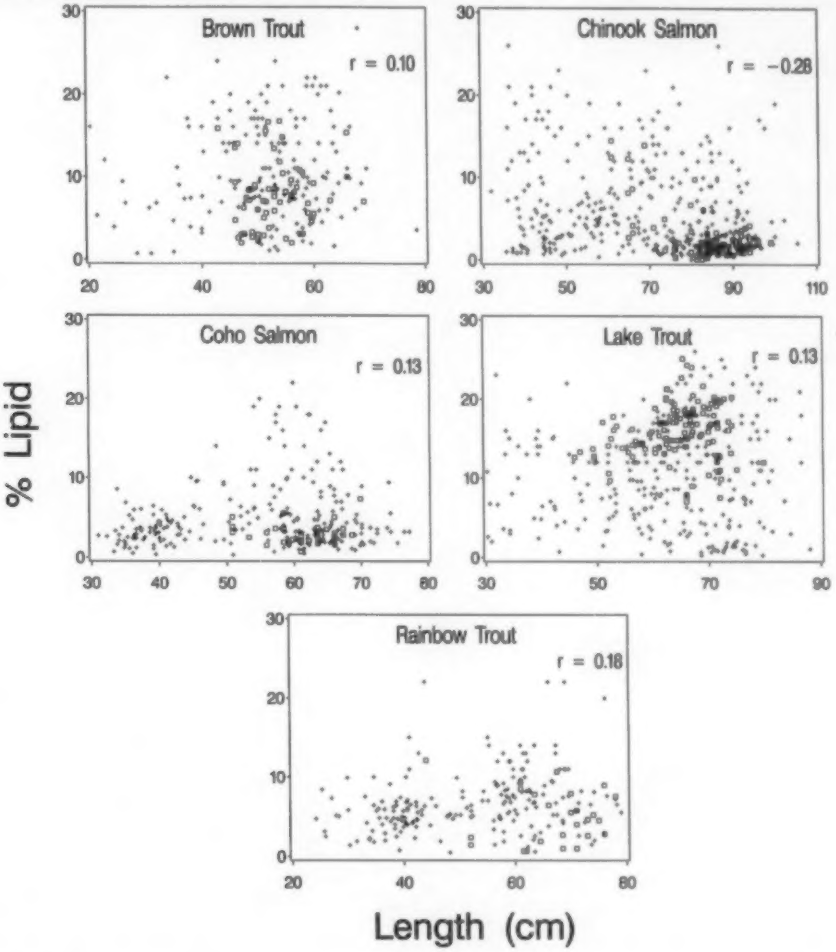
Previous researchers have also indicated a minimal contaminant:lipid lake trout relationship. Weininger (1978) concluded that "Lake trout PCB concentration is functionally independent of fat content." Borgmann and Whittle (1991) concluded that lipid concentrations were not the major factor controlling contaminants in Lake Ontario lake trout, but that lipid might have some effect on contaminant excretion. In a comparison of Lake Superior lake trout subspecies, Miller et al. (1992) reported no discernible PCB bioaccumulation difference between the lean versus the fatty (siscowet) varieties.

In contrast, Rasmussen et al. (1990) concluded lipid to be important for predicting lake trout PCB concentrations. In their analysis, based on sample mean data, they were explicitly aware of the confounding (collinear) effects of lipid with size but for predictive purposes chose a lipid-based model, in lieu of a size-based model, because the lipid model predicted PCBs better in other species. However, they also suggested that size would be more important in an analysis of individuals and our results support their suggestion.

Although contaminant accumulation in lipid has been demonstrated by several researchers, it is worth noting that at least one study reported contaminants to be proportionally less that would be expected in the fatty tissue. Voiland et al. (1991) found that trimming fatty tissue from brown trout fillets reduced lipid concentrations by an average of 61.8%, while PCBs were reduced by 45.6% and mirex by 44.2%. This result suggests that contaminants were actually in higher proportion in the leaner tissue.

Hebert and Haffner (1991) found that contaminants in several cyprinids were not consistent with what would be predicted by fugacity-based bioaccumulation models and suggested that lipid concentration may provide the potential

Fig. 4. Percent lipid versus length for each of the five salmonid species. Symbols indicate Wisconsin Department of Natural Resources data (pluses) and Michigan Department of Natural Resources data (squares).



for bioaccumulation but that differential contaminant exposure, resulting from varying habitats, was more important. Our results do not support their bioaccumulation potential argument because all five salmonids have individuals exhibiting relatively low lipid levels and high PCB levels (Fig. 2). Habitat, however, may be very important as indicated by the "statistical significance" of location for all five salmonids.

This analysis is not without caveats. A more definitive argument could be made using data from whole-body analyses rather than skin-on fillets. We note, however, that Borgmann and Whittle (1991) reached conclusions consistent with ours, based on whole-body lake trout samples, and the positive PCB:lipid associations identified by Larsson et al. (1996) occurred in muscle tissue, a portion less likely to be consistent with whole-body relationships than the skin-on fillets used in our analysis.

We have also considered the possibility that the relative lack of a discernible PCB:lipid relationship could result from measurement error. Measurement error in the predictor variable (lipid) could cause the PCB:lipid slope estimator to be biased toward zero, essentially obscuring any relationship. This is known as the effect of "errors-in-variables" (Fuller 1987). When this occurs, the slope estimator is attenuated, under some fairly general conditions, by the following ratio:

$$\frac{\hat{\beta}_1 = \beta_1\sigma_\varepsilon^2}{\sigma_\varepsilon^2 + \sigma_\delta^2}$$

where $\hat{\beta}_1$ is the slope estimator, β_1 is the true slope value, σ_ε^2 is what the sample variance would be in the absence of measurement error, and σ_δ^2 is the measurement error variance. The denominator, $\sigma_\varepsilon^2 + \sigma_\delta^2$, is the total measured sample variance. When σ_δ^2 is small relative to $\sigma_\varepsilon^2 + \sigma_\delta^2$, the bias effect is minor. Conversely, when σ_δ^2 is relatively large, the bias is large. If it is reasonable to assume that σ_δ^2 is essentially constant among species, then we would expect the bias effect to be least pronounced in the species with the highest measured lipid variance because the ratio of $\sigma_\delta^2 + \sigma_\varepsilon^2 + \sigma_\delta^2$ would be smallest. However, in the species with the highest measured lipid variance, lake trout (measured lipid variance = 38.2), we actually

Table 1. ANOVA tables for the regression of log total PCB on year, location, log length, and log lipid for brown trout, chinook salmon, coho salmon, lake trout, and rainbow trout (year and location are included as classification variables).

	Source	df	Sum of squares	Mean square	F-value	P-value	R^2
Brown trout	Model	21	52.18	2.48	14.72	<0.0001	0.61
	Error	198	33.43	0.17			
	Corrected total	219	85.61				
	Year	6	15.45	2.57	15.25	<0.0001	
	Location	10	9.78	0.98	5.80	<0.0001	
	Log length	1	11.51	11.51	68.20	<0.0001	
	Log lipid	1	0.77	0.77	4.54	0.03	
Chinook salmon	Model	21	191.35	9.11	47.78	<0.0001	0.70
	Error	430	82.01	0.19			
	Corrected total	451	273.37				
	Year	7	7.93	1.13	5.94	<0.0001	
	Location	11	26.00	2.36	12.39	<0.0001	
	Log length	1	87.71	87.71	459.85	<0.0001	
	Log lipid	1	5.71	5.71	29.94	<0.0001	
Coho salmon	Model	17	77.60	4.56	16.23	<0.0001	0.52
	Error	251	70.60	0.28			
	Corrected total	268	148.19				
	Year	7	16.79	2.40	8.53	<0.0001	
	Location	8	10.04	1.25	4.46	<0.0001	
	Log length	1	41.50	41.50	147.56	<0.0001	
	Log lipid	1	3.94	3.94	14.01	0.0002	
Lake trout	Model	19	197.07	10.37	47.02	<0.0001	0.70
	Error	376	82.94	0.22			
	Corrected total	395	280.01				
	Year	8	29.85	3.73	16.92	<0.0001	
	Location	9	30.59	3.40	15.41	<0.0001	
	Log length	1	143.40	143.40	650.07	<0.0001	
	Log lipid	1	0.03	0.03	0.15	0.70	
Rainbow trout	Model	18	136.53	7.59	16.13	<0.0001	0.59
	Error	201	94.53	0.47			
	Corrected total	219	321.07				
	Year	6	23.05	3.84	8.17	<0.0001	
	Location	8	38.32	4.79	10.19	<0.0001	
	Log length	1	5.60	5.60	11.91	0.0007	
	Log lipid	1	0.31	0.31	0.65	0.42	

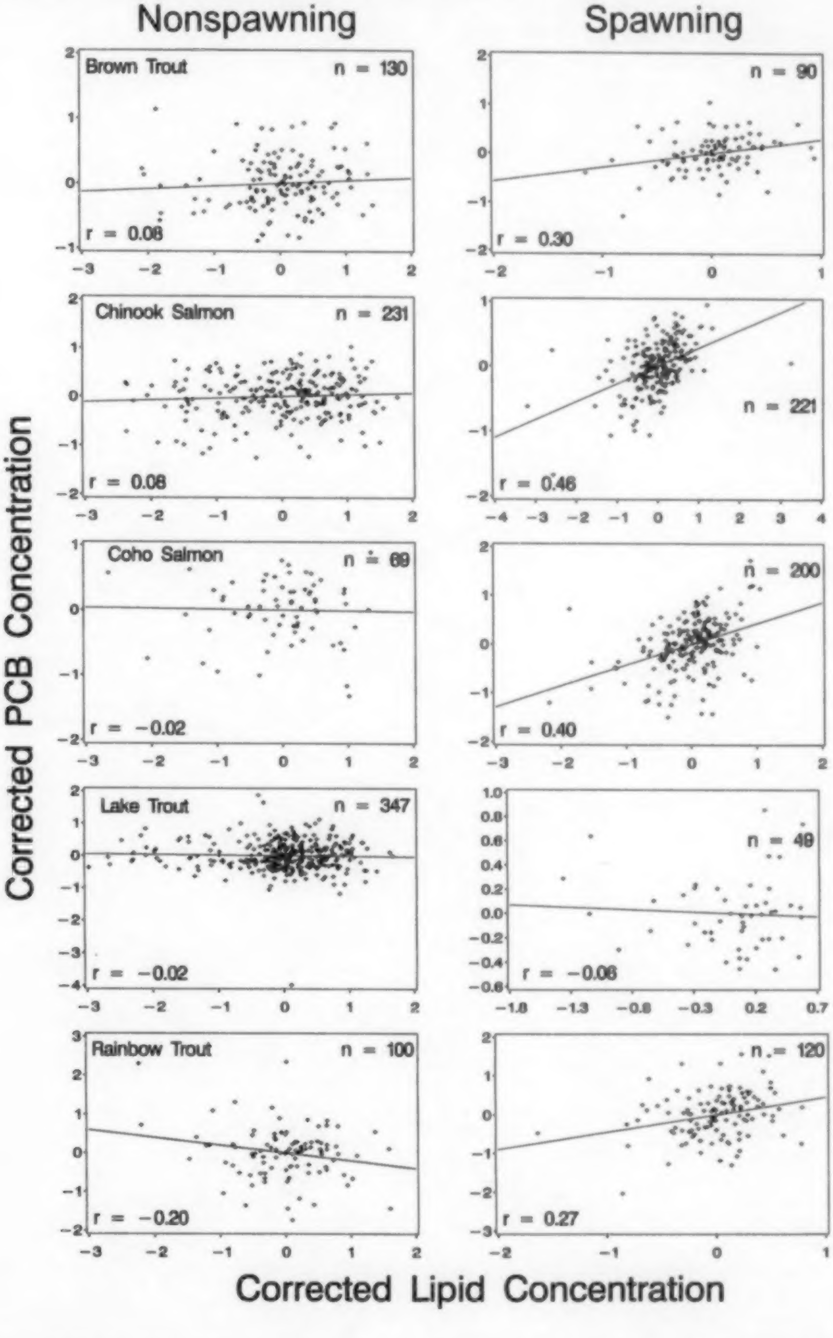
see the least relationship. Chinook, with a lower lipid variance (29.6), have a fairly pronounced relationship. Our data, then, appear to show exactly the opposite of what would be expected if measurement error were important, and therefore, we do not believe that measurement error is responsible for the patterns (or relative lack of patterns) we have identified.

We also point out that a positive PCB:lipid relationship could occur as an artifact of the analytical method. Lipid and PCB analyses are often not independent; they are typically performed on subsamples of the same extract. A varying extraction efficiency could influence both results similarly and induce an apparent positive relationship.

Why, then, have we not observed a PCB:lipid relationship except in spawning fish? Ewald and Larsson (1994) found that fish high in phospholipid accumulated less of a radiolabeled PCB congener than fish low in phospholipid. Their result, however, was reported as a difference between species, not within a species. An analogous difference in lipid type could occur among individuals. It is also possible that internal transport and deposition of contaminants is not strictly a passive process. Perhaps body tissues besides lipids harbor hydrophobic contaminants. While our analysis does not answer this question, it does indicate that factors other than lipid content are important in contaminant uptake and accumulation.

Hebert and Keenleyside (1995) discussed potential pitfalls associated with lipid normalizing contaminant data where lipid and contaminant concentrations do not covary. But what are the consequences if a relationship exists, and the observed correlation is spurious? More precisely, how is mechanistic inference affected if the cause–effect relationship is attributable to extraneous variables (Wonnacott and Wonnacott 1985)? Mean PCB and lipid values for the data in this study are highly correlated (Fig. 1). However, a similar relationship between species occurs with age. Coho live, at most, for 2 yr once they are stocked and chinook live, at most, 4 yr, while lake trout may live for more than 9 yr (Stewart and Ibarra 1991). Rainbow trout typically live about 4 yr in the lake, although they may live in streams before entering the lake (Seelbach 1993). Brown trout are reported to live up to 18 yr (Becker 1983), although this is probably an extreme. Age is a plausible extraneous variable, previously identified as an important PCB concentration determinant (Madenjian et al.

Fig. 5. Residuals from the regression of log PCB on year, location, and log length versus residuals from the regression of log lipid on year, location, and log length for nonspawning and spawning individuals. These plots depict the relationship between log PCB concentration and log lipid concentration, for each salmonid species, with the influence of the other variables removed.



1994), that may be responsible for the relationship in Fig. 1. Indeed, within species, length is a close surrogate for age.

Our empirical analysis indicates that PCB:lipid relationships are not as consistent as generally believed. While contaminants may accumulate in fatty tissue within a fish, this relationship is not strongly reflected among individuals in these data. Perhaps lipids play a role in contaminant accumulation differences between species, as one might infer from aggregate data (Fig. 1), but how this might occur between species and not individuals is difficult to reconcile.

Analysis of summary statistics can sometimes reveal patterns obscured by noisy data. However, aggregation of data can also discard considerable information. We suggest that these data contain an important message in the noise.

The relationship we have identified between PCB:lipid associations and spawning is interesting and may be an important piece of the puzzle concerning the role of lipids in contaminant bioaccumulation. Additional investigation of this phenomenon may provide useful insights.

Acknowledgments

We thank Chris Wood of the Michigan Department of Natural Resources for providing data. Jon Manchester-Neesvig, Tara Stow, and two anonymous reviewers provided helpful reviews of the manuscript. This work was funded by the University of Wisconsin Sea Grant Institute under grants from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, and the State of Wisconsin. Federal grant NA90AA-D-SG469, project R/MW-41.

References

Barber, M.C., Suarez, L.A., and Lassiter, R.R. 1991. Modelling bioaccumulation of organic pollutants in fish with an application to PCBs in Lake Ontario salmonids. Can. J. Fish. Aquat. Sci. **48**: 318–337.

Becker, G.C. 1983. Fishes of Wisconsin. The University of Wisconsin Press, Madison, Wisc.

Borgmann, U., and Whittle, D.M. 1991. Contaminant concentration trends in Lake Ontario lake trout (*Salvelinus namaycush*): 1977 to 1988. J. Great Lakes Res. **17**: 368–381.

Ewald, G., and Larsson, P. 1994. Partitioning of ^{14}C-labelled 2,2′,4,4′-tetrachlorobiphenyl between water and fish lipids. Environ. Toxicol. Chem. **13**: 1577–1580.

Food and Drug Administration. 1977. Pesticide analytical manual. Vol. I. U.S. Department of Health Education and Welfare, Washington, D.C.

Fuller, W.A. 1987. Measurement error models. John Wiley & Sons, New York.

Gobas, F.A.P.C., Zhang, X., and Wells, R. 1993. Gastrointestinal magnification: the mechanism of biomagnification and food chain accumulation of organic chemicals. Environ. Sci. Technol. **27**: 2855–2863.

Hamelink, J.L., Waybrant, R.C., and Ball, R.C. 1971. A proposal: exchange equilibria control the degree chlorinated hydrocarbons are biologically magnified in lentic environments. Trans. Am. Fish. Soc. **100**: 207–214.

Hebert, C.E., and Haffner, G.D. 1991. Habitat partitioning and contaminant exposure in cyprinids. Can. J. Fish. Aquat. Sci. **48**: 261–266.

Hebert, C.E., and Keenleyside, K.A. 1995. To normalize or not to normalize? Fat is the question. Environ. Toxicol. Chem. **14**: 801–807.

Larsson, P., Backe, C., Bremle, G., Eklov, A., and Okla, L. 1996. Persistent pollutants in a salmon population (*Salmo salar*) of the southern Baltic Sea. Can. J. Fish. Aquat. Sci. **53**: 62–69.

Leblanc, G.A. 1995. Trophic-level differences in the bioconcentration of chemicals: implications in assessing environmental biomagnification. Environ. Sci. Technol. **29**: 154–160.

Madenjian, C.P., Carpenter, S.R., and Rand, P.S. 1994. Why are the PCB concentrations of salmonine individuals from the same lake so highly variable? Can. J. Fish. Aquat. Sci. **51**: 800–807.

Miller, M.A. 1993. Maternal transfer of organochlorine compounds in salmonines to their eggs. Can. J. Fish. Aquat. Sci. **50**: 1405–1413.

Miller, M.A., Madenjian, C.P., and Masnado, R.G. 1992. Patterns of organochlorine contamination in lake trout from Wisconsin waters of the Great Lakes. J. Great Lakes Res. **18**: 742–754.

Niimi, A.J., and Oliver, B.G. 1983. Biological half-lives of polychlorinated biphenyl congeners in whole fish and muscle of rainbow trout (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. **40**: 1388–1394.

Niimi, A.J., and Oliver, B.G. 1989. Distribution of polychlorinated biphenyl congeners and other halocarbons in whole fish and muscle among Lake Ontario salmonids. Environ. Sci. Technol. **23**: 83–88.

Price, H.A., Welch, R.L., Scheel, R.H., and Warren, L.A. 1986. Modified multiresidue method for chlordane, toxaphene, and polychlorinated biphenyls in fish. Bull. Environ. Contam. Toxicol. **37**: 1–9.

Rasmussen, J.B., Rowan, D.J., Lean, D.R.S., and Carey, J.H. 1990. Food chain structure in Ontario lakes determines PCB levels in lake trout (*Salvelinus namaycush*) and other pelagic fish. Can. J. Fish. Aquat. Sci. **47**: 2030–2038.

Reinert, R.E. 1969. Insecticides and the Great Lakes. Limnos, **2**: 3–9.

Reinert, R.E. 1970. Pesticide concentrations in Great Lakes fish. Pestic. Monit. J. **3**: 233–240.

Reinert, R.E., Stewart, D., and Seagran, H.L. 1972. Effects of dressing and cooking on DDT concentrations in certain fish from Lake Michigan. J. Fish. Res. Board Can. **29**: 525–529.

Rowan, D.J., and Rasmussen, J.B. 1992. Why don't Great Lakes fish reflect environmental concentrations of organic contaminants? An analysis of between-lake variability in the ecological partitioning of PCBs and DDT. J. Great Lakes Res. **18**: 724–741.

SAS Institute Inc. 1987. SAS/STAT guide for personal computers, version 6. SAS Institute Inc., Cary, N.C.

Seelbach, P.W. 1993. Population biology of steelhead in a stable-flow, low-gradient tributary of Lake Michigan. Trans. Am. Fish. Soc. **122**: 179–198.

Skea, J.C., Simonin, H.A., Harris, E.J., Jacking, S., Spagnoli, J.J., Symula, J., and Colquhoun, J.R. 1979. Reducing levels of Mirex, Aroclor 1254, and DDE by trimming and cooking Lake Ontario brown trout (*Salmo trutta* Linnaeus) and smallmouth bass (*Micropterus dolomieui* Lacépède). J. Great Lakes Res. **5**: 153–159.

Stewart, D.J., and Ibarra, M. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978–88. Can. J. Fish. Aquat. Sci. **48**: 909–922.

Stow, C.A. 1995. Factors associated with PCB concentrations in Lake Michigan salmonids. Environ. Sci. Technol. **29**: 522–527.

Stow, C.A., Carpenter, S.R., and Amrhein, J.F. 1994. PCB concentration trends in Lake Michigan coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*). Can. J. Fish. Aquat. Sci. **51**: 1384–1390.

Voiland, M.P., Gall, K.L., Lisk, D.J., and Macneill, D.B. 1991. Effectiveness of recommended fat-trimming procedures on the reduction of PCB and mirex levels in brown trout (*Salmo trutta*) from Lake Ontario. J. Great Lakes Res. **17**: 454–460.

Weininger, D. 1978. Accumulation of PCBs by lake trout in Lake Michigan. Ph.D. dissertation, University of Wisconsin–Madison, Madison, Wisc.

Weisberg, S. 1985. Applied linear regression. 2nd ed. John Wiley & Sons, New York.

Wonnacott, R.J., and Wonnacott, T.H. 1985. Introductory statistics. 4th ed. John Wiley & Sons, New York.

Responses of skin mucous cells to aluminum exposure at low pH in Atlantic salmon (*Salmo salar*) smolts

M.H.G. Berntssen, F. Kroglund, B.O. Rosseland, and S.E. Wendelaar Bonga

Abstract: Atlantic salmon (*Salmo salar*) smolts were exposed for 80 h to seven water qualities: pH 5.6 with 31 and 46 μg labile Al·L^{-1}, pH 6.0 with 18 and 24 μg labile Al·L^{-1}, and pH 6.2 with 12 and 18 μg labile Al·L^{-1} and control water at pH 6.8 and <10 μg labile Al·L^{-1}. The three groups with the highest concentrations of labile Al (31 and 46 μg labile Al·L^{-1} at pH 5.6 and 24 μg labile Al·L^{-1} at pH 6.0) suffered high mortalities and showed a disturbance in osmoregulation and a massive secretion of mucus, as seen from a decrease in number of skin mucous cells. Furthermore, an increase in skin mucous cells containing acidic mucosubstances was observed. The loss of plasma chloride and skin mucous cells showed a significant linear correlation ($R^2 = 0.68$, $p < 0.001$). The increased secretion of mucus on skin and gills and the increase in acidity of mucosubstances are consistent with their prior presumed defensive role in binding of Al.

Résumé : Des smolts de saumon atlantique (*Salmo salar*) ont été exposés pendant 80 h à sept environnements différents pour ce qui est de la qualité de l'eau : pH 5,6 avec 31 et 46 μg Al labile·L^{-1}, pH 6,0 avec 18 et 24 μg Al labile·L^{-1} et pH 6,2 avec 12 et 18 μg Al labile·L^{-1} et une eau témoin à pH 6,8 avec < 10 μg Al labile·L^{-1}. Les trois groupes présentant les concentrations les plus élevées d'Al labile (31 et 46 μg Al labile·L^{-1} à pH 5,6 et 24 μg Al labile·L^{-1} à pH 6,0) ont éprouvé une mortalité élevée ainsi qu'une perturbation de l'osmorégulation et une sécrétion massive de mucus, comme en témoigne une diminution du nombre de cellules muqueuses cutanées. De plus, une augmentation du nombre de cellules muqueuses cutanées contenant des mucosubstances acides a été observée. La perte de chlorure plasmatique et de cellules muqueuses cutanées montrait une corrélation linéaire importante ($R^2 = 0{,}68$, $p < 0{,}001$). La sécrétion accrue de mucus sur la peau et dans les branchies et l'augmentation de l'acidité des mucosubstances sont en accord avec le rôle antérieure présumé de protection en fixant l'Al. [Traduit par la Rédaction]

Introduction

Acidification of freshwater causes an increase in dissolved Al as a result of Al leaching from soil and sediment (Schofield and Trojnar 1980; Overrein et al. 1981). Although low water pH can have negative effects on fish physiology (Packer and Dunson 1970; Brown 1981) and low Ca concentrations exacerbate the toxicity of acidified freshwater (McDonald et al. 1980; Rosseland 1989), Al is considered to be the main toxic component in acidified environments (Leivestad et al. 1987; McWilliams 1990; Spry and Weiner 1991). The toxicity of Al is dependent on its aqueous speciation which is dependent on pH, temperature, and the presence of organic and inorganic substances (Howells et al. 1990; Rosseland and Staurnes 1994). Inorganic monomeric Al is believed to be the most toxic Al species (Driscoll et al. 1980) which is the predominant monomeric Al fraction at pH 4.5–5.5. (Lydersen et al.1990). However, recently it has been established that Al toxicity can also be high at high pH when Al-rich acid water mixes with neutral water. The rapid increase in pH in such a mixing zone causes Al polymerisation and subsequently severe stress and mortality in fish (Rosseland et al. 1992). For anadromous species such as the Atlantic salmon (*Salmo salar*), the smolt stage is considered particularly sensitive to low pH/Al exposure (Rosseland and Skogheim 1984; Rosseland et al. 1986*b*; Skogheim and Rosseland 1986) because of the extensive changes in physiology for preadaptating them to marine life (Staurnes et al. 1993).

Osmotic failure is considered to be one of the main toxic mechanisms in salmonids exposed to Al at low pH (Leivestad et al. 1987). A loss in plasma ions in low pH/Al stressed fish is, in the short term, mostly associated with an increase in blood haematocrit (Malte 1986; Audet and Wood 1988; Wood et al. 1988). Another prominent characteristic of fish exposed to low pH/Al is the stimulated secretion of mucus (Muniz and Leivestad 1980; Leivestad 1982; Rosseland and Skogheim 1984; Youson and Neville 1987) and the change in chemical composition of mucus on the skin (Zuchelkowski et al. 1985; Iger et al. 1994) and gills (Mueller et al. 1991). The role of this mucus secretion and the change in chemical composition of mucus during acid exposure has been suggested to be an adaptive response to prevent osmoregulatory failure (Solanski and Benjamin 1982; Zuchelkowski et al. 1985; Jagoe and Haines 1990) or to reduce Al accumulation on the gill epithelium (Mueller et al. 1991; Wilkinson and Campbell 1993).

The mucification of acid-exposed fish in short-term exposures (within the first day of exposure) is correlated with a

Received April 1, 1996. Accepted October 7, 1996.
J13383

M.H.G. Berntssen[1] **and S.E. Wendelaar Bonga.** Department of Animal Physiology, Faculty of Science, University of Nijmegen, Toernooiveld, 6525 ED Nijmegen, The Netherlands.
F. Kroglund. Norwegian Institute for Water Research, Regional Office Grimstad, Televeien 1, 4890 Grimstad, Norway.
B.O. Rosseland. Norwegian Institute for Water Research, P.O. Box 173 Kjelsås, 0411 Oslo, Norway.

[1] Present address: Institute of Nutrition, Directorate of Fisheries, P.O. Box 185. N-5002 Bergen, Norway. e-mail: spor_mb@nutr.fiskeridir.no

Table 1. Water chemistry (means ± SD, $n = 3$, temperature = 10.5°C) of the experimental and reference water.

Condition (pH/Al addition)	pH	Ca (mg·L^{-1})	Acid-reactive Al (μg·L^{-1})	Nonlabile Al (μg·L^{-1})	Labile Al (μg·L^{-1})
Control	6.8	3.6±0.03	<10	<10	<10
pH 6.2/low Al	6.2	2.4±0.04	55.6±3.5	44.0±5.7	11.5±2.1
pH 6.2/high Al	6.2	2.4±0.04	71.6±5.0	53.5±0.7	18.0±4.2
pH 6.0/low Al	6.0	2.4±0.03	54.5±5.0	37.0±7.1	17.5±2.1
pH 6.0/high Al	6.0	2.4±0.03	76.0±1.4	52.5±2.1	23.5±0.7
pH 5.6/low Al	5.6	2.1±0.03	68.5±2.1	37.5±7.1	31.0±0.0
pH 5.6/high Al	5.6	2.1±0.03	91.0±2.8	45.5±2.1	45.5±5.0

reduction in mucous cells due to the exhausted secretion of the mucous cells (Iger et al. 1988, 1994). In long-term exposures (over 4 d; Iger et al. 1994), the mucification is thought to be due to hyperplasia of mucous cells in skin and gills (Zuchelkowski et al. 1981; Jagoe and Haines 1990). To our knowledge, the early reduction in number of mucous cells has never been applied as a quantitative parameter of the mucus secretion in low pH/Al exposed salmonids during the early phase of exposure, i.e., when rapid ion loss takes place.

The objectives of this study were to (*i*) characterise the initial mucous secretion and composition of skin mucus after low pH/Al exposure, by quantification of skin mucous cells, and (*ii*) document a concentration–response effect on mucification in correlation with ion regulation in the early stages of different low pH/Al combinations.

Materials and methods

Experimental conditions and protocol

Fish used were 1-yr-old smoltifying Atlantic salmon from the River Imsa strain. For smolts, mean ± SD of length (fork length), mass, and condition factor were 17.6 ± 0.7 cm, 49.8 ± 4.7 g, and 0.89 ± 0.04 g·cm^{-3}, respectively ($n = 210$). These fish were raised at the Freshwater Research Station at Ims from the Norwegian Institute of Nature Research and were kept for 2.5 d before the experiment in their experimental tanks (80 fish per tank) in neutral water in order to acclimate (pH 6.75, Ca = 3.56 ± 0.03 mg·L^{-1}, total Al < 10 mg·L^{-1}, temperature 10.5°C). In one of the experimental tanks, this water quality was maintained during the entire experiment as a control. The experimental tanks had a volume of 80 L with a flow rate of 2.3 L·min^{-1}, creating enough counterflow to give the fish natural swimming movement. During the entire experiment (80 h) the fish were not fed. A photoperiod regime of 16 h of light and 8 h of darkness was maintained.

Six different water qualities were made by mixing acid Al-rich tap water (pH 5.0, Ca = 1.8 ± 0.02 mg·L^{-1}, total Al = 74.0 ± 2.8 mg·L^{-1}, labile Al = 40.5 ± 5.0 mg·L^{-1}) and water from the River Imsa (pH 6.8, Ca = 3.56 ± 0.03 mg·L^{-1}, total Al < 10 mg·L^{-1}, labile Al < 10 mg·L^{-1}) in three separate main tanks (90 L), resulting in water with pH levels of 6.2, 6.0, and 5.6, respectively. From here, water from each main tank was distributed to two supplementary tanks (20 L), one of which was given extra Al (to give an addition of 23 μg total Al·L^{-1} in the exposure tanks). The water from these supplementary tanks was delivered to the exposure tanks. The succession of the main and supplementary tanks assured a residence time of about 20 min·tank^{-1} for proper mixing of the water.

After starting exposure of the fish, samples were taken after approximately 0, 6, 17, 55, and 80 h. The sampled fish were killed by a blow to the head, weighed, and their fork lengths measured. Immediately afterwards, blood samples were taken from the caudal vessels by severing the tail. Haematocrit was determined immediately (standard MSE microhaematocrit centrifuge type 346, 3 min). Blood samples were centrifuged (Hettich EBA type 3, 2450 RCF (g) for 5 min) and immediately analysed for plasma Cl (Radiometer CMT 10, chloride titrator). During the course of the experiment, cumulative mortalities were recorded every fourth hour.

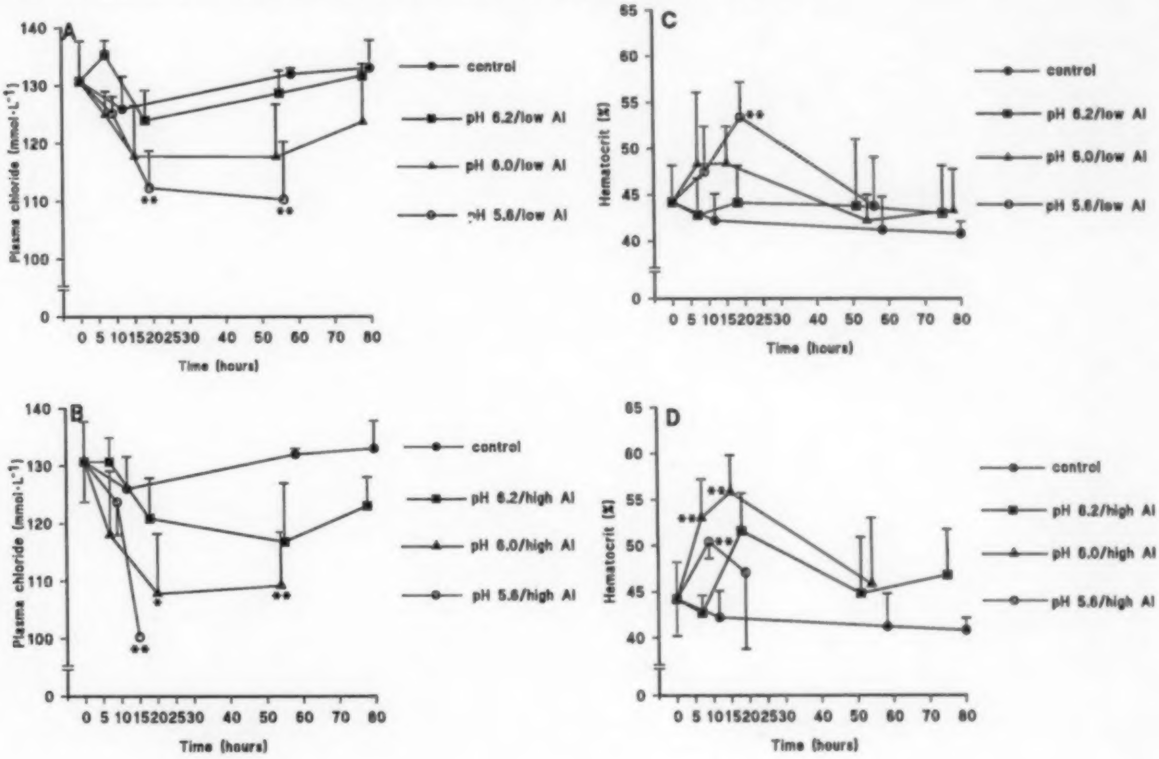
Histology and tissue processing

A small piece of skin was taken from the ventral side near the head. This part of the skin has few scales and is therefore appropriate for histological analysis. Care was taken not to damage the skin during sampling. The skin samples were fixed for 24 h in Bouin's fixative (volume ratio of picric acid – formaldehyde – acetic acid = 15:5:1); afterwards the samples were washed three times in 70% ethanol and preserved in 90% ethanol. After routine dehydration in alcohol series, the samples were embedded in paraffin wax (oriented vertically) and 5-mm cross sections were cut with a microtome (MOD.1330/Biocut) (Ferguson et al. 1992). Special care was taken to cut the sections consistently in a plane perpendicular to the surface of the epidermis. The sections were stained with Alcian blue at pH 2.6 (AB.2), haemalum, and eosin. The AB.2 was used to identify the mucous cells containing acid glycoprotein (Jones and Reid 1973): AB.2-positive mucous cells have an acid, negatively charged mucus content, and AB.2-negative mucous cells contain more neutral mucosubstances. The sections were examined with a Zeiss light microscope at 400× magnification. A Mertz linear grid was used to, planimetrically, quantify the number of mucous cells per 0.1-mm transect of skin epithelium; 12 cross sections were examined per fish, and six fish per group were examined randomly. Because the thickness of the epidermis in the exposed groups did not change (this was determined by measuring the epidermal height at both ends and in the middle of a 0.1-mm transect in 12 cross sections per fish), the density of the mucous cells was expressed as number of cells per 0.1 mm. Mucous cells were identified as large swollen cells with a basal located nucleus. Mucous cells with acid glycoproteins stained deep blue with AB.2.

Water chemistry

Temperature and pH were measured three times a day (Orion model 207 pH meter with a Riadometer glass electrode) during the experiment. For Al speciation, water samples were collected ($n = 3$), stored at low temperature (4°C), and subjected to Al speciation analyses in the laboratory of the Norwegian Institute for Freshwater Research according to the EN 45000 standards. Al was analysed by the pyrocatechol-violet method (Dougan and Wilson 1974) adapted for automatic analysis by Henriksen and Bergmann-Paulsen (1975), and the fraction obtained without any pretreatments was denoted acid-reactive Al. The acid-reactive fraction is presumed to contain the total monomeric Al. Water samples were fractionated over a cation-exchange column using the procedure of Driscoll (1980), modified for FIA by Røgeberg and Henriksen (1985). The Al in the eluate was called nonlabile Al and is presumed to primary include organically complexed monomeric Al (Rosseland et al. 1986*a*). The concentration of labile or inorganic monomeric Al was calculated from the

Fig. 1. Plasma Cl⁻ (A) without and (B) with an addition of 23 mg total Al·L^{-1} and haematocrit (C) without and (D) with an addition of 23 mg total Al·L^{-1} (mean ± SD, $n = 6$) for smolts of Atlantic salmon exposed for 80 h to low pH/Al water. Lines with open symbols represent the groups with significantly different values from the values of the control group: $*p < 0.05$; $**p < 0.01$.



difference between acid-reactive Al and nonlabile Al (Rosseland et al. 1986*a*). Ca was analysed on ICP.

During the mixing of Al-rich acid water and neutral water, total Al concentrations increased and Ca concentration decreased with lowering pH. The addition of 23 mg total Al·L^{-1} resulted in elevated labile Al concentrations at all pH levels (high Al groups), with an especially high increase in labile Al at lower pH (e.g., a 25% increase in labile Al at pH 6.05 and a 32.8% increase in labile Al at pH 5.6; Table 1).

Statistics

Data are presented as means ± SD. Overall differences between groups were assessed by analysis of variance (ANOVA), with time and treatment (pH, Ca, and Al addition) as independent variables. Significance was tested using Tukey's test ($p < 0.01$ and $p < 0.05$). Best correlation between variance and factors (pH, Ca, acid-reactive Al, nonlabile Al, and labile Al) was assessed by matrix correlation followed by multiple regression analysis. The correlation curves were fitted with the regression program FIG.P. 6.0.

Results

No mortality was observed for fish held in pH 6.8 (control), pH 6.0, and pH 6.2/low Al (<10, 17.5, and 11.5 μg labile Al·L^{-1}, respectively). The addition of Al at pH 6.0 (23.5 μg labile Al·L^{-1}) resulted in a LT$_{50}$ of 36 h. Both the pH 5.6/low and high Al groups (31 and 45.5 μg labile Al·L^{-1}, respectively) showed high mortality, with LT$_{50}$'s of 60 and 29 h, respectively.

At the start of the experiment the plasma Cl⁻ and haematocrit levels were 130 ± 5 mmol·L^{-1} and 43 ± 7%, respectively. Plasma Cl⁻ and haematocrit levels in control fish did not change significantly during the experiment. After 16 h the pH 5.6/low and high Al and the pH 6.0/high Al groups had a significantly lower plasma Cl⁻ than controls and remained low during the rest of the experiment (Figs. 1A and 1B). In all exposure groups the heamatocrit values increased initially, reaching highest values after 15 h after which they returned to control levels (Figs. 1C and 1D). The pH 6.0/high Al and pH 5.6/low and high Al groups differed significantly from the controls after 7 h (Fig. 1C).

The mucous cells in the skin of our Atlantic salmon corresponded with the description Daye and Garside (1980) for this species. The total number of skin mucous cells showed a rapid initial decrease in the first 16 h for all groups, except the controls and the pH 6.2 and pH 6.0/low Al groups. The rapid decrease slowed down later (Figs. 2A and 2B). After 16 h of exposure in the pH 5.6/low and high Al and the pH 6.0/high Al groups, the number of skin mucous cells was significantly lower than in controls; the reduction in skin mucous cells was 40% for both the pH 5.6 and pH 6.0/high Al groups and 27% for the pH 5.6/low Al group. Along with the loss of skin mucous cells, the Atlantic salmon smolts held in the three acute toxic water qualities (pH 5.6/high and low Al and pH 6.0/high Al) developed a visible thick layer of mucus on the skin and coagulates of mucus on the edges of the opercula within the

Fig. 2. Number of mucous cells in the skin (A) without and (B) with addition of 23 mg total $Al \cdot L^{-1}$ and ratio of AB.2-positive to AB.2-negative mucous cells (C) without and (D) with addition of 23 mg total $Al \cdot L^{-1}$ (mean ± SD, $n = 6$) for smolts of Atlantic salmon exposed for 80 h to water of different pH and Al concentrations. Lines with open symbols represent the groups with significantly different values from the values of the control group: $*p < 0.05$; $**p < 0.01$.

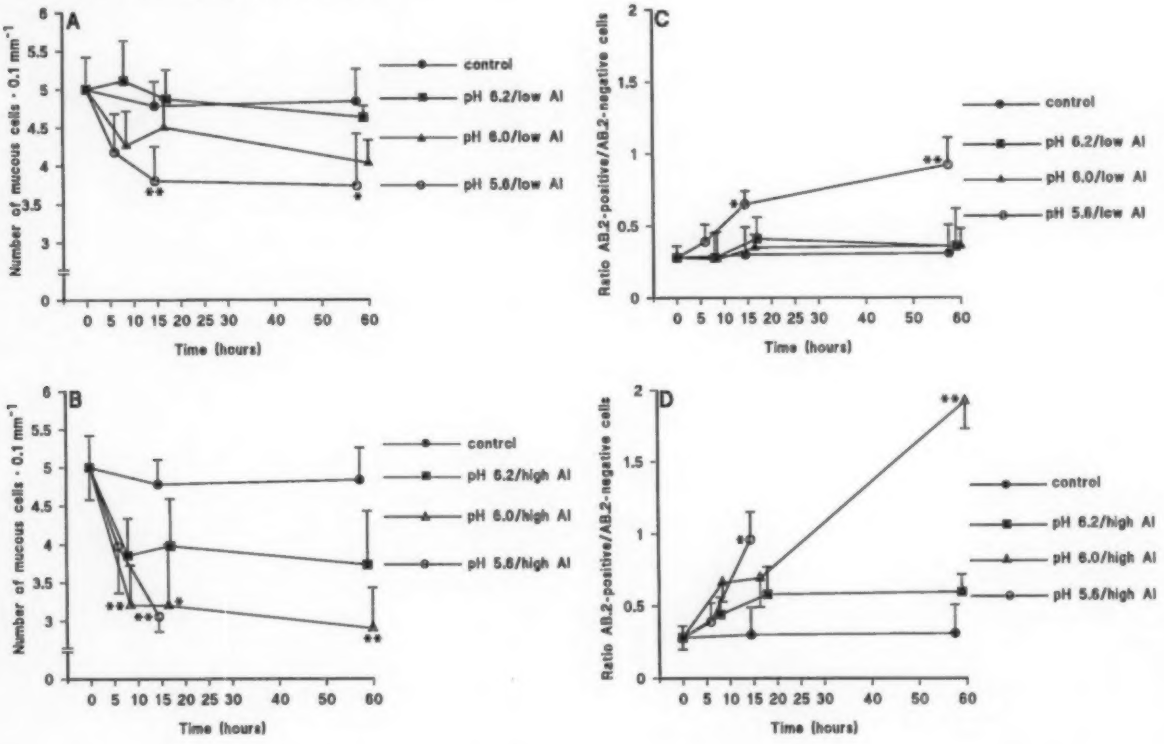
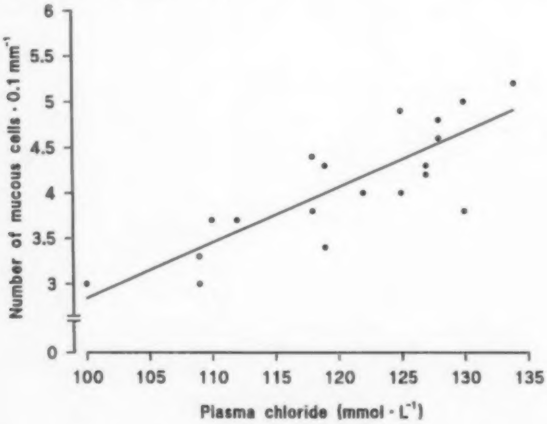


Fig. 3. Correlation between plasma Cl^- concentration and number of skin mucous cells; regression line: skin mucous $= 0.61 \cdot Cl^- - 3.24$, $R^2 = 0.68$, $p < 0.001$.



first phase of exposure. The number of skin mucous cells of control fish did not change significantly during the experiment. Furthermore, an increase in the ratio of AB.2-positive to AB.2-negative mucous cells was observed for fish from the pH 5.6/low and high Al and pH 6.0/high Al groups (Fig. 2C).

Both the decrease in number of mucous cells and the loss of plasma Cl^- were correlated with an increase in labile Al (multiple regression analysis, $p < 0.01$). Plasma Cl^- levels decreased in direct proportion to the decrease in the number of mucous cells (Fig. 3A; $R^2 = 0.68$, $p < 0.001$).

Discussion

At the start of the experiment the plasma Cl^- and haematocrit levels were similar to those in smolts of the same strain in neutral water (Rosseland and Skogheim 1984). The loss of plasma Cl^- and increase in haematocrit were already initiated at labile Al concentrations of 24 $mg \cdot L^{-1}$ at pH 6.0 and a Ca concentration of 2.35 $mg \cdot L^{-1}$. These results agree with the study of Rosseland et al. (1986*a*), who documented plasma Cl^- loss (from 110 to 85 $mmol \cdot L^{-1}$) for Atlantic salmon smolts exposed to 21.5 mg labile $Al \cdot L^{-1}$ at pH 6.6 and 2.68 mg $Ca \cdot L^{-1}$. The mixing of acid-rich tap water with neutral river water in the supplementary tanks implies that we cannot exclude a possible toxic influence from ongoing Al polymerisation (Rosseland et al. 1992). However, this is unlikely because no toxic effects were observed in brown trout (*Salmo trutta*) exposed to a 5.6-min aged mixing zone (Verbost et al. 1995). The retention time of 20 min of the mixed water in this experiment was considered long enough to diminish possible toxic effects of mixing before the water entered the exposure tanks.

In addition, both the decrease in number of mucous cells and the loss of plasma Cl^- were significantly ($p < 0.01$) correlated with an increase in labile Al. The labile Al concentration in the exposure tanks was therefore considered to be the predominant toxic Al fraction.

High mortalities were observed in the three exposure groups with the highest concentrations of labile Al (pH 5.6/low and high Al and pH 6.0/high Al). These groups were also characterised by a disturbance in osmoregulation (decrease in plasma Cl^- values with a subsequently increased haematocrit) and a reduced number of skin mucous cells. No significant difference in plasma Cl^-, haematocrit, or number of skin mucous cells was observed between these three groups, suggesting that these concentrations of labile Al caused a maximum stress response resulting in high mortality.

The reduction in number of mucous cells is probably the result of exhaustion of the mucous cells caused by extensive mucus secretion (Iger et al.1988, 1994; Roy 1988). The strong decrease in skin mucous cells was associated with a general mucification of gills and skin, and this indicates that the number of skin mucous cells is a good parameter for quantification of mucus secretion.

The initial rapid exhaustion of the mucous cells is apparently not compensated by formation of new skin mucous cells within the 80 h of exposure. This indicates a long generation time, and this is in line with data from the literature. Generation of new skin mucous cells takes 5–6 d in carp (*Cyprinus carpio*) (Iger et al. 1988), Arctic char (*Salvelinus alpinus*) (Pickering and Macey 1977), and brown trout (Pickering et al. 1982). Other authors, however, observed hyperplasia within the first 2 d of acid exposure in the gills of rainbow trout (*Oncorhynchus mykiss*) (Audet and Wood 1993) and in the skin of brown bullhead (*Ictalurus nebulosus*) (Zuchelkowski et al. 1986). The observed increase in mucous cell numerical densities in these studies might reflect a proliferation of immature mucous cells which is not dominated by a loss of mucous cells due to a massive discharge of their contents. Iger et al. (1994) described a first-phase response of skin mucous cells in acid-exposed fish by migration of the mucous cells towards the epidermal surface combined with increase in cell volume. This could result in an increase in the number of identifiable mucous cells. If the rapid depletion of the mucous cells is not compensated for by formation of new cells, this will lead to reduced mucus secretion. Since body mucus has an important role for protection against pathogens or toxicants (Shephard 1994), exposure to low pH with Al could make the fish more vulnerable to these agents.

The groups with a significantly fewer number of mucous cells also had an increased ratio of AB.2-positive to AB.2-negative cells, indicating a relative increase in skin mucous cells containing acid glycoproteins (Ferguson et al. 1992). In contrast, Iger et al. (1994) reported an increase of mucous granules with more neutral glycoproteins in the skin of rainbow trout exposed to acid water. However, in their study the increase in mucous granules with neutral glycoproteins occurred after 4 d of exposure whereas the relative decrease in neutral glycoproteins in our study was observed within the first 3 d of exposure. Because mucus is initially synthesised as neutral glycoproteins (Mittal et al. 1980) and the differentiation of new mucous cells takes 5–6 d (Pickering and Macey 1977; Pickering et al. 1982; Iger et al. 1988), the increase in neutral glycoproteins in the studies of Iger et al. (1994) might reflect a differentiation of new mucous cells after depletion of mucous cells in the first phase of exposure. Reid et al. (1991) found a reduced gill sialic acid content after 8 d of low pH/Al exposure in rainbow trout. Because sialoglycoproteins are a major component of the mucus layer (Fletcher et al. 1976), this reduced gill sialic acid might reflect a relative increase in neutral glycoproteins similar to the observations of Iger et al. (1994). The accuracy of measurement of mucus content, by a component such as sialic acid (Harris et al. 1973), may be influenced by changes in the chemical composition of the mucus (McDonald et al. 1991). The change in ratio in our study could reflect stimulated differentiation of new mucous cells with acid-rich glycoproteins or an increase of acid glycoproteins in already formed mucous cells. The latter process was the most likely in the present study because the differentiation of new mucous cells took longer than the 80 h of exposure time. Mittal et al. (1980) stated that fully differentiated mucous cells can increase the degree of sulfating of their glycoproteins. In addition, Zuchelkowski et al. (1985) found an increased sulfation of mucosubstances after 24 h in acid-exposed brown bullhead. This process of enhanced sulfation in mature mucous cells will subsequently lead to an increased release of mucus containing more acid glycoproteins.

In earlier studies on brook trout (*Salvelinus fontinalis*) exposed to low pH/Al, Booth et al. (1988) divided the ionoregulatory response into two relatively distinct phases: an initial "shock" phase characterised by a loss in blood ions and a "recovery" phase where surviving fish showed some recovery. In our study the shock phase was characterised by a rapid loss in plasma Cl^- and a subsequent increase in haematocrit during the first 16 h, with no recovery of the plasma Cl^- values during the remainder of the exposure period. The ion-regulatory shock phase of low pH/Al exposure appeared to be associated with the decrease in the number of mucous cells. A linear correlation ($R^2 = 0.68$, $p < 0.001$) was found between the decrease in plasma Cl^- (indicating osmoregulatory failure) and the decrease in the number of skin mucous cells.

These results coincide with the presumed adaptive function for mucus secretion in the response of fish to low pH/Al exposure, as was suggested before by several authors (Shephard 1994). A function of mucus in prevention of an osmotic disturbance by Al exposure, e.g., by forming a diffusion barrier to passive plasma ion movement across the skin and gill membrane or to concentrated cations near the epithelial surface to aid the active uptake of ions, seems to be unlikely because Na^+,Cl^-, and Ca^{2+} diffusion is not substantially affected by mucus layers, as measured on dilute solutions of mucus (Marshall 1978; Pärt and Lock 1983; Stith 1984). More likely, mucus has an indirect function by retarding Al diffusion from the solution to the membrane surface, thus reducing the negative impact of Al on the epidermal surface (Wilkinson and Campbell 1993). Wilkinson and Campbell (1993) observed a high absorption of gill-associated Al in the mucus and not to the gill surface itself, resulting in the largest accumulation of Al in the mucus layer. This accumulated Al can be readily eliminated from gill surface by high secretion of mucus (McDonald et al. 1991; Mueller et al. 1991) coupled with increased rate of mucus sloughing (Leivestad 1982; Neville and Campbell 1988; Wilkinson and Campbell 1993), thus reducing Al damage or accumulation on the gill surface that may cause the ionoregulatory disturbance. The relative increase in AB.2-positive mucous cells observed in our study could subsequently lead to secretion of more negatively charged mucus. Since most accumulated Al is probably absorbed to the gill surface by binding to negatively charged groups of the mucus layer (Reid et al. 1991; Wilkinson and Campbell 1993), the relative increase in mucous cells containing acid glycoproteins could enhance the retention of Al in the mucous layer.

Excessive secretion of mucus, together with a precipitation of Al, however, might lead to clogging of the gills and respiratory problems (Leivestad 1982; Witters et al. 1996). The greater mucus production with deposition of Al can increase the resistance to O_2 and CO_2 diffusion and subsequently lead to respiratory dysfunction (Witters et al. 1996). Leivestad (1982) found an excessive mucus secretion and glogging on the gill with hyperventilation and reduced venous oxygen pressure in low pH/Al exposed brown tout. In addition, Witters et al. (1996) observed an increased ventilation frequency with gill mucification after exposing brown trout to Al in a toxic mixing zone.

The present study showed that the decrease in the number of skin mucous cells is associated with the overall mucification of skin and gills in the first phase of Al exposure, which is characterised by a rapid disturbance of ion regulation. The increase in secretion of mucus and change in mucus chemistry support the presumed defence role of mucus against Al toxicity.

Acknowledgements

We thank Dr. P.M. Verbost, University of Nijmegen, for giving valuable comments on the manuscript and Dr. Å. Åtland, Norwegian Institute of Nature Research, for assistance in the practical work and for commenting on the manuscript. This study was financed by the Norwegian Directorate for Nature and Management, the Norwegian Institute for Water Research, and by a grant from the Dutch Technology Foundation (STW) (project NBI 22.2832).

References

Audet, C., and Wood, C.M. 1988. Do rainbow trout (*Salmo gairdneri*) acclimate to low pH? Can. J. Fish. Aquat. Sci. **45**: 1399–1405.

Audet, C., and Wood, C.M. 1993. Branchial morphological and endocrine responses of rainbow trout (*Oncorhynchus mykiss*) to a long-term sublethal acid exposure in which acclimation did not occur. Can. J. Fish. Aquat. Sci. **50**: 198–209.

Booth, C.E., McDonald, D.G., Simons, B.P., and Wood, C.M. 1988. Effects of aluminum and low pH on net ion fluxes and ion balance in the brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. **45**: 1563–1574.

Brown, D.J.A. 1981. The effects of various cations on the survival of brown trout, *Salmo trutta*, at low pH's. J. Fish Biol. **18**: 31–40.

Daye, P.G., and Garside, E.T. 1980. Structural alterations in embryos and alevins of the Atlantic salmon, *Salmo salar* L., induced by continuous or short-term exposure to acidic levels of pH. Can. J. Zool. **58**: 27–43.

Dougan, W.K., and Wilson, A.L. 1974. The absorptiometric determination of aluminium in water. A comparison of some chromogenic reagents and the development of an improved method. Analyst, **99**: 413–430.

Driscoll, C.T. 1980. Chemical charaterization of some dilute acidified lakes and streams in the Adirondack Region of New York State. Ph.D. thesis, Cornwell University, Ithaca, N.Y.

Driscoll, C.T., Baker, J.P., Bisogni, J.J., Jr., and Schofield, L. 1980. Effects of aluminium speciation on fish in dilute acidified waters. Nature (Lond.), **284**: 161–164.

Ferguson, H.W., Morrison, D., Ostland, V.E., Lumsden, J., and Byrne, P. 1992. Responses of mucus producing cells in gill disease of rainbow trout (*Oncorhynchus mykiss*). J. Comp. Pathol. **106**: 255–265.

Fletcher, T.C., Jones, R., and Reid, L. 1976. Identification of glycoproteins in globet cells of epidermis and gill of plaice (*Pleuronectes plattessa*) and rainbow trout (*Salmo gairdneri*). Histochem. J. **8**: 597–608.

Harris, J., Watson, A., and Hunt, S. 1973. Histochemical analysis of mucous cells in the epidermis of brook trout, *Salmo trutta* L. J. Fish Biol. **5**: 345–351.

Henriksen, A., and Bergmann-Paulsen, I.M. 1975. An automatic method for determining aluminium in natural waters. Vatten, **4**: 339–342.

Howells, G., Dalziel, T.R.K., Reader, J.P., and Solbe, J.F. 1990. EIFAC water quality criteria for European freshwater fish: report on aluminium. Chem. Ecol. **4**: 117–173.

Jagoe, C.H., and Haines, T.A. 1990. Morphometric effects of low pH and limed water on the gills of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **47**: 2451–2460.

Jones, R., and Reid, L. 1973. The effects of pH on Alcian blue staining of the epithelial acid glycoproteins 1. Sialomucins and sulphomucins (singly or in simple combinations). Histochem. J. **5**: 9–18.

Iger, Y., Abraham, M., Dotan, A., Fattal, B., and Rahamin, E. 1988. Cellular responses in the skin of carp maintained in organically fertilised water. J. Fish Biol. **33**: 711–720.

Iger, Y., Balm, P.H.M., and Wendelaar Bonga, S.E. 1994. Cellular responses of the skin and changes in plasma cortisol levels of trout (*Oncorhynchus mykiss*) exposed to acidified water. Cell Tissue Res. **278**: 535–542.

Leivestad, H. 1982. Physiological effects of acid stress on fish. *In* Proc. Int. Symp. Acid Rain Fish. Impacts in North Eastern America. *Edited by* R.E. Johnson. American Fisheries Society, Bethesda, Md. pp. 157–163.

Leivestad, H., Jensen, E., Kjartansson, H., and Xingfu, L. 1987. Aqueous speciation of aluminium and toxic effects on Atlantic salmon. Soc. R. Zool. Belg. **117**: 387–398.

Lydersen, E., Poleo, A.B.S., Muniz, I.P., Salbu, B., and Bjornstad, H.E. 1990. The effects of naturally occurring high and low molecular weight inorganic and organic species on the yolk-sac larvae of Atlantic salmon (*Salmo salar*) exposed to acidic aluminium-rich lake water. Aquat. Toxicol. **18**: 219–230.

Malte, H. 1986. Effects of aluminium in hard, acid water on metabolic rate, blood gas tensions and ionic status in the rainbow trout. J. Fish Biol. **29**: 187–198.

Marshall, W.S. 1978. On the involvement of mucous secretion in teleost osmoregulation. Can. J. Zool. **56**: 1088–1091.

McDonald, D.G., Hobe, H., and Wood, C.M. 1980. The influence of calcium on the physiological responses of the rainbow trout, *Salmo gairdneri*, to low environmental pH. J. Exp. Biol. **88**: 109–131.

McDonald, D.G., Wood, C.M., Rhem, R.G., Mueller, M.E., Mount, D.R., and Bergman, H.L. 1991. Nature and time course of acclimation to aluminum in juvenile brook trout (*Salvelinus fontinalis*). I. Physiology. Can. J. Fish. Aquat. Sci. **48**: 2006–2015.

McWilliams, P.G.L. 1990. Smolt production and water quality. Aspect of the physiology of Atlantic salmon (*Salmo salar*) eggs and fry with particular reference to water treatment on commercial smolt farms. Final report. Water Quality Project II (1986–89), Salar-BP Norway. University of Bergen.

Mittal, A.K., Whitear, M., and Agarwal, S.K. 1980. Fine structure and histochemistry of the epidermis of the fish *Monopterus cuchia*. J. Zool. Lond. **191**: 107–125.

Mueller, M.E., Sanchez, D.A., Bergman, H.L., McDonald, D.G., Rhem, R.G., and Wood, C.M. 1991. Nature and time course of acclimation to aluminum in juvenile brook trout (*Salvelinus fontinalis*). II. Gill histology. Can. J. Fish. Aquat. Sci. **48**: 2016–2027.

Muniz, I.P., and Leivestad, H. 1980. Toxic effect of aluminium on the brown trout, *Salmo trutta* L. *In* Proceedings of the International Conference on the Ecological Impact of Acid Precipitation. *Edited by* D. Drablos and A.Tollan. SNSF-Project, Oslo, Norway. pp. 320–321.

Neville, C.M., and Campbell, P.G.C. 1988. Possible mechanisms of aluminium toxicity in a dilute, acidic environment to fingerlings and older life stages salmonids. Water Air Soil Pollut. **42**: 311–327.

Overrein, L.S., Seip, H.M., and Tollan, A. 1981. Acid precipitation effects on forest and fish. Res. Rep. Fagrapp. FR 19/80. Final report of the SNSF-Project 1972–1980, Oslo, Norway.

Packer, R.K., and Dunson, W.A. 1970. Effects of low environmental pH on blood pH and sodium balance of brook trout. J. Exp. Zool. **174**: 65–72.

Pärt, P., and Lock, R.A.C. 1983. Diffusion of calcium, cadmium and mercury in a mucous solution from rainbow trout. Comp. Biochem. Physiol. C Comp. Pharmacol. **76**: 259–263.

Pickering, A.D., and Macey, D.J. 1977. Structure, histochemistry and the effect of handling on the mucous cells of the epidermis of the char *Salvelinus alpinus* (L.). J. Fish Biol. **10**: 505–512.

Pickering, A.D., Pottinger, T.G., and Christie, P. 1982. Recovery of the brown trout (*Salmo trutta*) from acute handling stress: a time-course study. J. Fish Biol. **20**: 229–244.

Reid, S.D., McDonald, D.G., and Rhem, R.R. 1991. Acclimation to sublethal aluminum: modification of metal–gill surface interactions of juvenile rainbow trout (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci. **48**: 1996–2005.

Røgeberg, E., and Henriksen, A. 1985. An automatic method for fractionation and determination of aluminium species in freshwater. Vatten, **41**: 48–53.

Rosseland, B.O. 1989. Kalking av rennende vann. Vurdering av toleransegrenser for laks og sjøørret ved driftstans av doseringsanlegg (Liming of running waters. Evaluation of tolerance levels for Atlantic salmon and sea trout at technical failure in limestone dosers). NIVA-rapport, Kalking av surt vann 5/89. p. 14. (In Norwegian.)

Rosseland, B.O., and Skogheim, O.K. 1984. A comparative study on salmonid fish species in acid aluminium-rich water. II. Physiological stress and mortality of one and two year old fish. Inst. Freshwater Res. Drottningholm Rep. **61**: 186–194.

Rosseland, B.O., and Staurnes, M. 1994. Physiological mechanisms for toxic effects and resistance to acidic water: an ecophysiological and ecotoxicological approach. *In* Acidification of freshwater ecosystems, implication for the future. *Edited by* C.E.W Steinberg and R.F. Wright. Environ. Sci. Res. Rep. ES 14, Wiley, Chichester. pp. 227–246.

Rosseland, B.O., Skogheim, O.K., Abrahamsen, H., and Matzow, D. 1986*a*. Limestone slurry reduces physiological stress and increases survival of Atlantic salmon (*Salmo salar*) in an acidic Norwegian river. Can. J. Fish. Aquat. Sci. **43**: 1888–1893.

Rosseland, B.O., Skogheim, O.K., Kroglund, F., and Hoell, E. 1986*b*. Mortality and physiological stress of year-classes of landlocked and migratory salmon, brown and brook trout in acid aluminium-rich water. Water Air Soil Pollut. **30**: 751–756.

Rosseland, B.O., Blaker, I., Bulger, A., Kroglund, F., Kvellstad, A., Lydersen, E., Oughton, D.H., Salbu, B., Staurnes, M., and Vogt, R. 1992. The mixing zone between limed and acidic river waters: complex aluminium chemistry and extreme toxicity for salmonids. Environ. Pollut. **78**: 3–8.

Roy, D. 1988. Statistical analysis of anionic detergent induced changes in the goblet mucous cells of opercular epidermis and gill epithelium of *Rita rita* (Ham.) (Bagridae: Pisces). Ecotoxicol. Environ. Saf. **15**: 260–271.

Schofield, C.L., and Trojnar, R.J. 1980. Aluminium toxicity to brook trout (*Salvelinus fontinalis*) in acidified waters. *In* Polluted rain. *Edited by* T.Y. Toribara, M.W. Miller, and P.E. Morrow. Plenum Press, New York. pp. 341–363.

Shephard, K.L. 1994. Functions for fish mucus. Rev. Fish Biol. Fish. **4**: 401–429.

Skogheim, O.K., and Rosseland, B.O. 1986. Mortality of smolt of Atlantic salmon (*Salmo salar*) at low levels of aluminium in acid soft waters. Bull. Environ. Contam. Toxicol. **37**: 258–256.

Solanski, T.G., and Benjamin, M.1982. Changes in the mucous cells of the gills, buccal cavity and epidermis of the nine-spined stickleback, *Pungitius pungitius* L., induced by transferring the fish to seawater. J. Fish Biol. **21**: 563–575.

Spry, D.J., and Weiner, G.J. 1991. Metal bioavailability and toxicity to fish in low-alkalinity lakes: a critical review. Environ. Pollut. **71**: 243–304.

Staurnes, M., Blix, P., and Reite, O.B. 1993. Effects of water and aluminum on parr–smolt transformation and seawater tolerance in Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. **50**: 1816–1827.

Stith, B.J. 1984. Effects of an external charged layer on transepithelial ion movement in frog skin. J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. **155**: 97–101.

Verbost, P.M., Berntssen, M.H.G., Kroglund, F., Lydersen, E., Witters, H.E., Rosseland, B.O., Salbu, B., and Wendelaar Bonga, S.E. 1995. The toxic mixing zone of neutral and acidic water: acute aluminium toxicity in brown trout (*Salmo trutta* L.). Water Air Soil Pollut. **85**: 341–346.

Wilkinson, K.J., and Campbell, P.G.C. 1993. Aluminium bioconcentration at the gill surface of juvenile Atlantic salmon in acid media. Environ. Toxicol. Chem. **12**: 2083–2095.

Witters, H.E., VanPuymbroeck, S., Stouthart, A.J.H.X., and Wendelaar Bonga, S.E. 1996. Physicochemical changes of aluminium in mixing zones: mortality and physiological disturbances in brown trout (*Salmo trutta* L.). Environ. Toxicol. Chem. **15**: 986–996.

Wood, C.M., Playle, R.C., Simons, B.P., Goss, G., and McDonald, D.G. 1988. Blood gasses, acid base, ions, and haematology in adult brook trout (*Salvelinus fontinalis*) under acid/aluminum exposures. Can. J. Fish. Aquat. Sci. **45**: 1575–1586.

Youson, J.H., and Neville, C.M. 1987. Deposition of aluminum in the gill epithelium of rainbow trout (*Salmo gairdneri* Richardson) subjected to sublethal concentration of the metal. Can. J. Zool. **65**: 647–656.

Zuchelkowski, E.M., Lantz, R.C., and Hinton, D.E. 1981. Effects of acid-stress on epidermal mucous cells of the brown bullhead *Ictalurus nebulosus* (LeSueur): a morphometric study. Anat. Rec. **200**: 33–39.

Zuchelkowski, E.M., Pinkstaff, C.A., and Hinton, D.E. 1985. Mucosubstance histochemistry in control and acid-stressed epidermis of brown bullhead catfish, *Ictalurus nebulosus* (LeSueur). Anat. Rec. **212**: 327–335.

Zuchelkowski, E.M., Lantz, R.C., and Hinton, D.E. 1986. Skin mucous cells response to acid stress in male and female brown bullhead catfish, *Ictalurus nebulosus* (LeSueur). Aquat. Toxicol. **8**: 139–148.

Toxicity and accumulation of zinc and copper in *Hyalella azteca* exposed to metal-spiked sediments

Uwe Borgmann and Warren P. Norwood

Abstract: The relationship between zinc and copper toxicity in *Hyalella azteca* and accumulation from metal-spiked sediments was determined for future use in identifying sites where these metals contribute to sediment toxicity. Both zinc and copper accumulation increased rapidly with increasing sediment concentrations, showing no evidence of saturation as seen in waterborne exposures. Zinc accumulation from zinc spiked sediments was substantial, even at concentrations below those causing chronic toxicity, and body concentrations can readily be used to infer chronic toxicity. Chronic toxicity in spiked sediment exposures occurred at excess (above background) body concentrations twice as high as in waterborne exposures, possibly as a result of zinc in gut contents. In contrast, chronic copper toxicity occurred at body concentrations lower than those observed in waterborne exposures. Furthermore, body copper at low sediment exposures was independent of copper in sediment. Body copper concentrations can be used to infer short-term (1-week) toxicity but not chronic toxicity. Copper, but not zinc, caused a reduction in growth, even at concentrations below the 4-week LC25. Reduced growth can, therefore, be used to differentiate between chronic copper and zinc toxicity in sediments.

Résumé : La relation entre la toxicité du zinc et du cuivre chez *Hyalella azteca* et l'accumulation à partir de sédiments dopés avec des métaux a été déterminée pour utilisation ultérieure dans l'identification des sites où ces métaux contribuent à la toxicité des sédiments. L'accumulation du zinc et celle du cuivre ont toutes deux augmenté rapidement par suite de l'augmentation de leur concentration dans les sédiments, en ne montrant aucune indication de saturation comme on le voit dans le cas de l'exposition par l'eau. L'accumulation du zinc à partir de sédiments dopés avec du zinc était substantielle, même à des concentrations inférieures à celles qui causent la toxicité chronique, et les concentrations corporelles peuvent être utilisées facilement pour déduire la toxicité chronique. La toxicité chronique dans les expositions par des sédiments dopés est survenue à des concentrations corporelles excessives (au-dessus du bruit de fond) deux fois plus élevées que dans le cas de l'exposition par l'eau, peut-être à cause du zinc dans le contenu intestinal. Par opposition, la toxicité chronique du cuivre s'est manifestée à des concentrations inférieures à celles observées dans les expositions par l'eau. De plus, le cuivre corporel provenant d'une faible exposition aux sédiments était indépendante de la concentration du cuivre dans les sédiments. Les concentrations corporelles de cuivre peuvent être utilisées pour déduire la toxicité à court terme (1 semaine), mais non la toxicité chronique. Le cuivre, mais non le zinc, a entraîné une réduction de la croissance, même à des concentrations inférieures à la CL25 de 4 semaines. Par conséquent, la réduction de la croissance peut servir à distinguer la toxicité du cuivre de celle du zinc dans les sédiments.
[Traduit par la Rédaction]

Introduction

A major problem in assessing the impact of pollution is identification of which chemicals, if any, are actually responsible for causing toxicity. Remedial actions will not be effective if the causative agents for environmental degradation are not identified correctly. Toxicity testing procedures have come a long way and can be used to demonstrate the presence, but not usually the identity, of toxic substances. The total concentration of a chemical in water or sediments is not a reliable indicator of biological effects, which are a function of a chemical's bioavailability (Luoma 1989; Ankley et al. 1994; Krantzberg 1994). Toxicity identification and evaluation procedures (Schubauer-Berigan et al. 1993; Ankley and Schubauer-Berigan 1995) are useful for identifying which chemicals are responsible for toxicity, but these can be complex and labour intensive procedures and ultimately require a means of clearly demonstrating the cause and effect relationship for the suspected agent. They also suffer from the disadvantage that they can only be used when significant toxicity occurs. Sometimes it is advantageous to know which chemicals are close to a toxic threshold to provide advance warning before toxicity develops.

Several authors have suggested that greater use should be made of contaminant concentrations in biota, rather than in water or sediments, to predict toxicity (Connolly 1985; Landrum et al. 1992; McCarty and Mackay 1993). Body concentrations are often better predictors of biological effects because factors affecting a chemical's bioavailability are already taken into account. For example, cadmium toxicity to *Hyalella azteca* in waters with varying degrees of complexing capacity, and in the presence and absence of sediments, is much more constant

Received April 18, 1996. Accepted October 7, 1996.
J13424

Uwe Borgmann[1,2] and Warren P. Norwood.[1] Department of Fisheries and Oceans, Great Lakes Laboratory for Fisheries and Aquatic Sciences, Burlington, ON L7R 4A6, Canada.

[1] Present address for both authors: National Water Research Institute, Environment Canada, Burlington, ON L7R 4A6, Canada.

[2] Author to whom all correspondence should be addressed. e-mail: uwe.borgmann@cciw.ca

Table 1. Summary of 1- and 4-week survival and mean sediment, final water, and body concentrations of zinc and copper averaged over all experiments for cotton gauze controls (no sediment) and sediments containing 0 to 100% metal spiked sediment. Means were computed after log transformation to normalize variances and then back transformed. The standard error of the log transformed data is also shown.

Percent spiked sediment	Percent survival ($N_0 = 80$)		Sediment concentration ($N = 4$)		Final water concentration ($N = 8$)		Body concentration		
	1-week	4-week	µmol/g(SE)	µg/g	µmol/L(SE)	µg/L	µmol/g(SE)	N	µg/g
Zinc									
Gauze	100	65	—	—	0.09 (0.219)	6	1.34 (0.019)	68	88
0	95	91	22.9 (0.063)	1499	1.83 (0.073)	117	2.30 (0.021)	70	151
10	95	86	36.3 (0.075)	2375	2.18 (0.085)	139	3.01 (0.020)	72	197
18	96	94	41.4 (0.019)	2705	2.61 (0.063)	166	4.10 (0.018)	72	268
32	94	33	70.0 (0.045)	4578	3.28 (0.122)	208	4.66 (0.027)	52	304
56	61	0	98.5 (0.044)	6443	8.27 (0.097)	525	9.01 (0.035)	32	589
100	1	0	128.1 (0.058)	8375	27.75 (0.169)	1763	8.09	1	529
Copper									
Gauze	100	65	—	—	0.06 (0.116)	4	1.33 (0.019)	72	85
0	95	91	1.2 (0.032)	74	0.24 (0.084)	15	2.41 (0.015)	62	153
3	98	95	4.7 (0.032)	300	0.54 (0.120)	34	2.40 (0.018)	40	152
6	100	78	5.7 (0.003)	363	0.67 (0.050)	42	2.30 (0.012)	39	146
10	96	45	17.6 (0.041)	1116	1.16 (0.104)	74	2.59 (0.015)	67	164
18	91	8	29.4 (0.036)	1868	1.41 (0.068)	90	3.88 (0.029)	38	247
32	29	0	42.1 (0.008)	2673	3.12 (0.040)	198	6.38 (0.026)	21	406
56	1	0	79.3 (0.002)	5038	4.32 (0.065)	275	11.68	1	742
100	0	0	143.9 (0.005)	9146	10.86 (0.022)	690	—	—	

if expressed on a body concentration basis rather than on a water concentration basis (Borgmann et al. 1991). Ultimately, toxicity is a function of a chemical's concentration at the site of toxic action and whole body concentrations will, therefore, only be good at predicting toxicity if there is a close correlation between whole-body concentrations and concentrations at the active site. The internal distribution of a contaminant can, unfortunately, be affected by its mode of uptake. For example, mercury is accumulated primarily in gills of mayflies during water exposure and primarily in the gut during exposure to contaminated sediments (Saouter et al. 1993). This could affect the whole-body concentration:toxicity relationship.

Hyalella azteca is the most widely distributed amphipod in North America (Bousfield 1958) and is extensively used in sediment toxicity testing (Borgmann and Munawar 1989; Ingersoll and Nelson 1990; American Society for Testing and Materials 1991; Ingersoll et al. 1995). The body concentration:toxicity relationship for zinc and copper during waterborne exposures have recently been evaluated in this species for future application in identifying toxic metals in environmental samples (Borgmann and Norwood 1995*a*). However, the applicability of these data to contaminated sediments, where accumulation could also occur through sediment ingestion, needs to be examined. The body concentration in *Hyalella* resulting in 50% mortality in chronic exposures to cadmium was about twice as high in contaminated sediment exposures as in water exposures (Borgmann et al. 1991), possibly because of contamination by gut contents or differences in internal distribution of the metal. This is a minor concentration difference for this metal. Cadmium concentrations in *Hyalella* from Ontario lakes can range over 400 fold (Stephenson and Mackie 1988). Zinc and copper, on the other hand, are essential metals and are regulated at low environmental concentrations (Borgmann and Norwood 1995*b*). Increases in body concentrations of only 2–3 fold are associated with toxicity (Borgmann et al. 1993; Borgmann and Norwood 1995*a*). Prediction of toxic effects from body concentration data, therefore, requires accurate data on body concentration:toxicity relationships and whether these are affected by waterborne versus contaminated sediment exposure. The purpose of this study was to determine the relationship between toxicity and accumulation of zinc and copper from contaminated sediments. The applicability of these data to the identification of the toxic agent in a field site is explored in a companion paper (Borgmann and Norwood 1997).

Methods

Amphipods were cultured as described in Borgmann et al. (1989). The water used for culturing and in experiments was Burlington city tap water (originating from Lake Ontario, hardness 130 mg/L, alkalinity 90 mg/L, pH 7.9–8.6) dechlorinated by bubbling with a standard aquarium charcoal filter. Cultures were examined and water was renewed weekly, providing a continuous supply of amphipods of known age for experiments. Cultures and experimental animals were kept in an incubator at 25°C with a 16 h light:8 h dark photoperiod.

Sediment was collected from site 1 in Hamilton Harbour with an Ekman sampler operated from a launch and stored in polyethylene buckets at 4°C until used. Site 1 is in the centre of the western end of the harbour. Sediment from this site consistently supported high survival in 4-week chronic toxicity tests over a 3-year period (Borgmann and Norwood 1993). It had a density of 1.22 g/mL, moisture content of 73%, and weight loss on ashing at 500°C was 9.1% of dry mass. Sediment was spiked with copper or zinc by mixing equal volumes of sediment and 50 mM $CuCl_2$ or $ZnCl_2$ in polypropylene bottles and rotating the mixture for 24 h at 4 rpm on a mechanical mixer. The metal spiking solutions were made with experimental water in an attempt to keep major ion concentrations as constant as possible. Sufficient concentrated HCl (230–330 µL/L) was added to dissolve the metal salts before mixing with the sediment. Control sediment was made by mixing equal volumes of sediment and acidified experimental water (300 µL HCl/L) and rotating on the same mixer with the metal spiked sediments. The sediment was allowed to settle and the excess water was decanted. Sufficient NaOH was added to neutralize the HCl originally added. Spiked sediments of lower concentration were then made by mixing 10, 18, 32, or 56% metal spiked sediments with control sediment. Copper spiked/control sediment mixtures of 3 and 6% were also made for the second experiments.

Toxicity tests were conducted as described in Borgmann and Norwood (1993). Sediment (40 mL) was carefully spooned into 250 mL beakers containing 160 mL of water. Beakers were covered with plastic petri dishes and gently aerated throughout the experiments. Twenty 0- to 1-week-old amphipods were added to each beaker for chronic (4 week) tests, and twenty 4- to 5-week-old amphipods were added for 1-week tests. Both chronic and 1-week experiments were repeated twice (initially in June–August 1994 and again in January–February 1995), with two replicate beakers for each metal concentration in each experiment. The water was not changed throughout the incubation period, but evaporated water was replaced with double-distilled water, as required. Approximately 5 mg of Tetra-Min fish food flakes was added to each test beaker as food, three times each week. After 1 or 4 weeks incubation, the surviving amphipods were sorted from the sediment by washing small portions of the sediment at a time into a plastic tray over a light table and counting the amphipods while removing them with a pipette. Surviving animals were rinsed in distilled water, dried at 60°C, and stored for metal analysis. With each experiment, an additional set of beakers was also set up containing cotton gauze instead of sediment. Amphipods were not placed in clean containers to allow clearance of sediment from the gut before drying because previous experiments indicated that zinc and copper in the body are lost rapidly (half life 4.3 days for Cu and 1.0 days for Zn, Borgmann and Norwood 1995*a*).

Individual dried amphipods (~0.5 mg dry mass) were digested with 12 µL of 70% nitric acid at room temperature for 1 week, after which 10 µL of 30% hydrogen peroxide was added and digestion was allowed to continue for another 24 h. Each sample was then made up to 0.5 mL with double-distilled water. Dried sediment samples were analyzed using the same dry mass:acid:peroxide ratio and digestion times, but with larger volumes (20 mg sediments, 500 µL nitric acid, 400 µL peroxide, 10 mL final volume). Samples of the overlying water were also taken at the end of the exposure period and acidified. Water, digested amphipods, and sediments were analyzed for zinc and copper on a Varian SpectraAA 400 graphite furnace atomic absorption spectrophotometer with Zeeman background correction. Copper was measured in a partition tube without modifier; zinc was analyzed using a platform and ammonium phosphate modifier.

Statistical analyses were performed by ANOVA using Systat 5.0. All metal concentration data were logarithmically transformed, and survival data were converted to mortality rates (log(survival)/time) and then log transformed before statistical analysis to equalize variances.

The 4-week LBC25 (Lethal Body Concentration resulting in 25% mortality) was computed to compare chronic toxicity in spiked sediment exposures to previously determined chronic toxicity in waterborne exposures. Chronic toxicity in the previous study had been quantified using the lowest effect concentration (Borgmann and Norwood 1995*a*). The lowest effect concentration is, however, an unreliable means of comparing different studies because the lowest concentration at which an effect is observable statistically is dependent on the variability in the data and the number of replicates. The previously determined lowest effect concentration (LEC) for waterborne exposures, expressed as excess (above background) body concentrations (Borgmann and Norwood 1995*a*), and the final survival after 4 and 10 weeks of exposure (assuming a constant mortality rate) are compared with the 4-week LBC25 below.

	10-week lowest effect concentration (µmol/g)	4-week LBC25 (µmol/g)	Percentage survival after 4 weeks at the LEC	Percentage survival after 10 weeks at the LEC
Zinc	1.27	1.49	86	69
Copper	1.80	1.90	79	56

A constant mortality rate resulting in a 4-week LBC25 will give 49% survival by week 10. A 4-week LBC25 will, therefore, provide a concentration slightly above the lowest effect concentration, which can be measured in 10-week exposures with *Hyalella* under the conditions and degree of replication used in these experiments.

Results

Measured zinc and copper concentrations in the mixed sediments were linearly related to the percentage of spiked sediment added (Table 1). Concentrations were 128 µmol Zn/g and 144 µmol Cu/g dry mass in 100% spiked sediment. Zinc concentrations in the control sediment (23 µmol/g) were much higher than copper (1.2 µmol/g). Control sediment concentrations were almost identical to those measured previously from Hamilton Harbour site 1 sediments (Borgmann and Norwood 1993).

Survival

Survival decreased with increasing metal concentrations, and results from the second experiment closely matched those from the first, even though these were done half a year later (Fig. 1). The only discrepancy was at 32% of maximum zinc (70 µmol/g), where 65% survived in the first chronic experiment and 0% in the second. As expected, amphipods tolerated significantly less metal in sediment during 4-week as compared with 1-week exposures.

Metal accumulation

In contrast with the survival curves, metal accumulation as a function of metal in the sediment was similar for both the 1-week and chronic exposures (Fig. 2). This agrees with previous observations that metal uptake from water equilibrates within 1 week (Borgmann and Norwood 1995*a*). Regression of logarithmically transformed data resulted in the following relationships:

$$(1) \quad Zn_{\mathrm{TB}} = Zn_{\mathrm{Bk}} + Zn_{\mathrm{Xs}} = 1.34 + 0.020 \cdot Zn_{\mathrm{sed}}^{1.26}$$

$$(2) \quad \begin{aligned} Cu_{\mathrm{TB}} &= Cu_{\mathrm{Bk}} + Cu_{\mathrm{Xs}} \\ &= 1.33 + 0.015 \cdot Cu_{\mathrm{sed}}^{1.54} \qquad Cu_{\mathrm{sed}} > 18\ \mu\mathrm{mol/g} \\ &= 2.38 \qquad\qquad\qquad\qquad Cu_{\mathrm{sed}} < 18\ \mu\mathrm{mol/g} \end{aligned}$$

where the subscript TB refers to total body metal concentration, Bk refers to the background concentration measured in animals exposed only to cotton gauze, Xs refers to metal accumulated in the body above background, and sed refers to sediment metal concentrations (all in µmol/g dry mass). Background concentrations were similar to those measured previously (Borgmann and Norwood 1995*b*). If data from the gauze-exposed animals were omitted and background concentrations were extrapolated by fitting the above equations to data from only sediment exposed *Hyalella*, then Zn_{Bk} was estimated at 1.14 and Cu_{Bk} at 1.57 µmol/g; neither value is significantly different from that measured in the gauze-exposed animals. Both zinc and copper in *Hyalella* increased rapidly with increasing sediment concentrations above 18 µmol/g in the sediment. However, copper concentrations in *Hyalella* were independent of copper in sediment between 1.2 and 18 µmol/g; mean body copper concentration was 2.38 µmol/g, averaged over the 0, 3, and 6% spiked sediment treatments, and not significantly higher (2.59 µmol/g) in the 10% spiked

Fig. 1. Survival of *Hyalella azteca* in separate experiments (indicated by different symbols) after exposure to zinc (A) and copper (B) spiked sediments as a function of measured metal concentrations in sediments in 1-week (▲ and ▼) and 4-week (■ and ◆) exposures. See text for explanation of fitted curve.

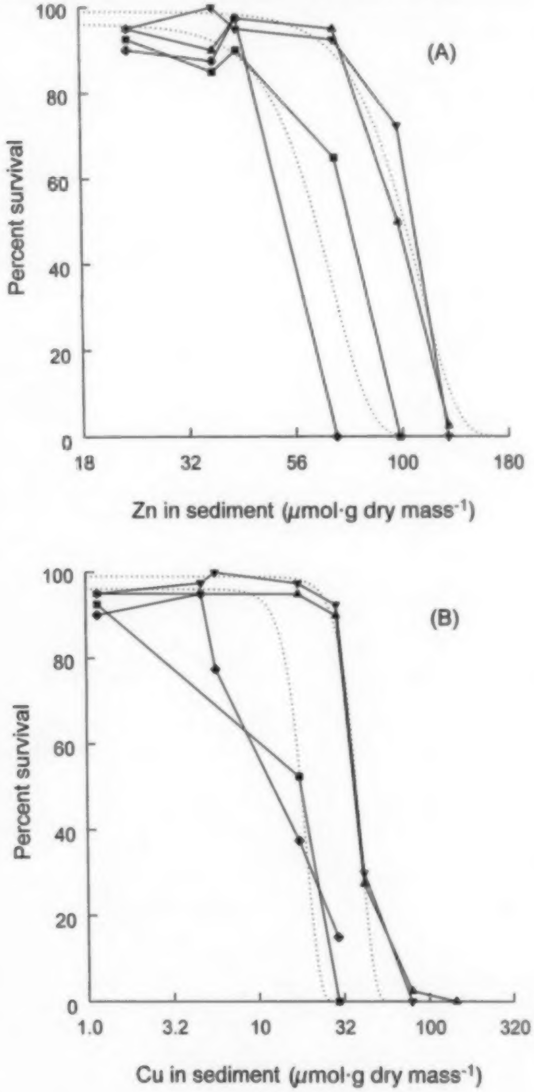
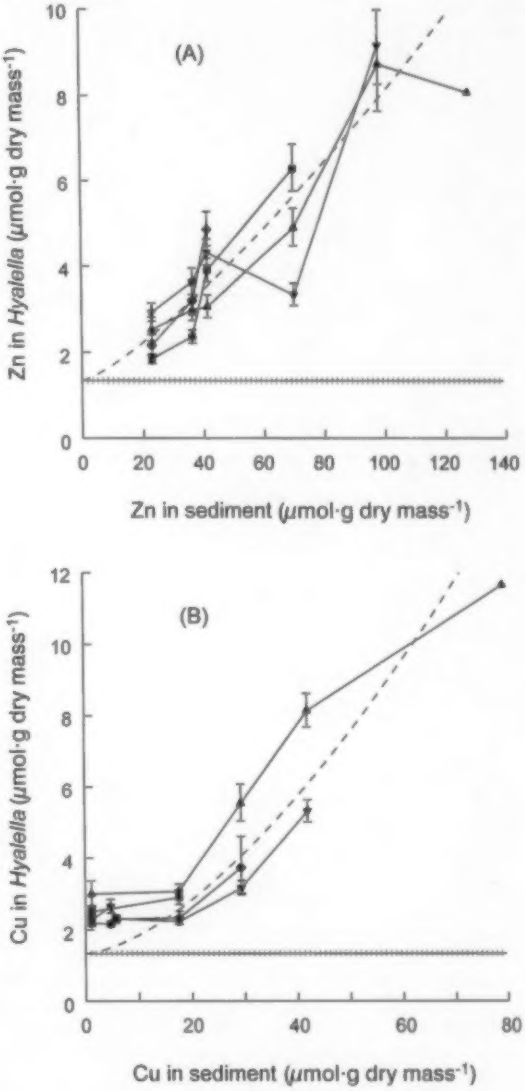


Fig. 2. Accumulation of zinc (A) and copper (B) by *Hyalella* from metal-spiked sediments in 1-week (▲ and ▼) and 4-week (■ and ◆) exposures. Metal concentrations in control amphipods exposed only to cotton gauze are indicted by the horizontal line (± 1 SE is indicated by dotted lines for control animals and error bars for sediment exposed animals). The dashed curve is given by eqs. 1 and 2 in the text.



sediment. Furthermore, copper concentrations in *Hyalella* exposed to control sediment were substantially higher ($P < 0.01$) than those given cotton gauze but no sediment (1.33 μmol/g, Table 1). Amphipods obviously accumulated copper from sediment, even in control sediment, but uptake appears to be regulated in some fashion until copper in sediment exceeds 18 μmol/g. Both zinc and copper concentrations in the overlying water increased with increasing sediment concentration (Table 1). The water:sediment concentration relationship for copper did not show the clear break seen in the body:sediment concentration relationship, suggesting that the body:sediment relationship is not due to a binding of copper to sediment which saturates at 18 μmol/g in the sediment.

Zinc concentrations in *Hyalella* were significantly elevated, relative to those in *Hyalella* exposed to control sediment, at all treatments above control, including those below which any toxic effect was observed in chronic or 1-week exposures. However, chronic toxicity was observed at 18 μmol Cu/g in the sediment, even though copper in *Hyalella* was not significantly elevated in this treatment relative to control sediment

Table 2. Chronic toxicity of zinc and copper in contaminated sediment exposures, compared with waterborne exposures (Borgmann et al. 1993; Borgmann and Norwood 1995*a*, 1995*b*), on a sediment or water (4-week LC25 or EC25) and body concentration (4-week LBC25 or EBC25)[a] basis. Also shown is the 4-week LBC50 and 1-week LBC25 and LBC50.

	Zinc		Copper	
	Waterborne exposure	Sediment exposure	Waterborne exposure	Sediment exposure
		Sediment concentrations (μmol/g DW)		
Control sediment	—	23	—	1.2
4-week LC25 (NOEC–LOEC)*b*	—	54 (41–70)	—	15.7 (5.7–17.6)
4-week EC25: mass (growth)	—	—	—	5.2 (4.7–5.7)
		Water concentrations (μmol/L)		
Background	0.086	0.094	0.055	0.058
Above control sediment	—	1.83	—	0.24
4-week LC25 (NOEC–LOEC)	1.70 (0.65–1.65)	3.29 (2.61–3.28)	0.33 (0.26–0.40)	1.36 (0.67–1.16)
4-week EC25: mass (growth)	—	—	—	0.59 (0.54–0.67)
		Body concentrations (μmol/g DW)		
Background	1.00	1.34	1.17	1.33
Excess metal (above background)				
Control sediment exposure	—	0.96	—	1.08
4-week LBC25 (NOEC–LOEC)	1.49 (1.3)	3.08 (2.76–3.32)	1.90 (1.8)	1.05 (0.97–1.26)
4-week LBC50	—	3.84	—	1.30
1-week LBC25 (NOEC–LOEC)	—	5.56 (3.32–7.67)	—	3.28 (2.55–5.05)
1-week LBC50	—	6.93	—	4.08
4-week EBC25: mass (growth)	—	—	—	1.05 (1.07–0.97)

[a] Lethal (or Effective) Body Concentration resulting in 25% mortality (or growth reduction).

[b] No observed effect concentration – lowest observed effect concentration.

(Table 2). Body copper was, however, significantly elevated in the next higher copper exposure (29 μmol/g sediment), which resulted in 92% mortality in 4 weeks, but negligible mortality within 1 week.

Toxicity:metal accumulation relationships

Survival was related to body concentration using the relationship

$$(3) \qquad m = m' + m'' = m' + a(C_{TB} - C_{Bk})^n$$

where m is the total instantaneous mortality rate (week^{-1}), m' is the control mortality rate, m'' is the toxicant induced mortality rate, and a and n are constants. One- and 4-week survival were computed from $e^{-m \cdot t}$, where t is time in weeks. In previous chronic toxicity experiments during exposures of *Hyalella* to waterborne Zn and Cu, n was estimated at 4 (Borgmann and Norwood 1995*a*). The value of the exponent n was difficult to estimate precisely in the present experiments because the rapid increase in mortality with increasing exposure resulted in few partial effect concentrations. However, a value of 4 seemed to fit the data reasonably well (Fig. 3) and is consistent with our previous estimate. Estimates of a were 0.0003 and 0.0008 for Zn in the 1- and 4-week sediment exposures, respectively, and 0.0025 and 0.06 for Cu in the 1- and 4-week exposures (Fig. 3). At $Cu_{Xs} < 1.05$ ($Cu_{TB} < 2.38$), a was equal to 0 in the 4-week exposure because of the apparent "regulation" of copper at 2.38 μmol/g in the body, resulting in the precipitous drop in the survival:body concentration relationship in Fig. 3B.

The body concentration:toxicity relationships (Fig. 3, eq. 3) were combined with the bioaccumulation relationship (Fig. 2, eqs. 1 and 2) to obtain the predicted sediment concentration:toxicity relationships shown by the dotted lines in Fig. 1. For this purpose the apparent "regulation" of copper was ignored. The exponential relationships for both mortality (eq. 3) and uptake (eq. 2) above 2.38 μmol Cu/g in *Hyalella* were extrapolated down to 0 μmol/g as if regulation did not occur; otherwise the toxicity curve below 18 μmol Cu/g in sediment cannot be predicted. The resultant curves fit the observed mortality fairly well, with the exception of one data point at low copper concentrations (Fig. 1).

Growth was affected by copper in the spiked sediments, but not by zinc (Fig. 4). Growth was, in fact, more sensitive to copper contamination than was survival. A substantial growth reduction occurred at 5.7 μmol Cu/g in the sediment, even though no chronic mortality was detected at this concentration. In contrast, there was no noticeable growth effect at 70 μmol Zn/g in the sediment, the highest concentration with some survival in the 4-week exposures. It is noteworthy that the reduced growth rate observed in copper spiked sediments was not observed in previous exposures of *Hyalella* to waterborne copper (Borgmann et al. 1993).

The 4-week LBC25 (computed using eq. 3) was twice as high for *Hyalella* exposed to zinc in sediments (3.08 μmol/g) as compared with zinc in water (Table 2). *Hyalella* therefore tolerates a higher body Zn concentration in sediment exposures. In exposures to copper spiked sediments, however, *Hyalella* suffers 25% mortality in 4 weeks at an excess body concentration of only 1.05 μmol Cu/g, lower than the body concentration resulting in similar mortality in waterborne exposures (1.90 μmol/g, Table 2). The 4-week LBC25 for copper falls within the flat portion of the uptake curve where copper uptake is independent of copper in sediment. Even the 4-week LBC50 represents an excess body concentration only slightly above that obtained in non-spiked sediment (1.30 μmol/g). A 25% reduction in final body size also falls

Fig. 3. Survival of *Hyalella* as a function of excess (above background) metal accumulated by amphipods in separate experiments after exposure to zinc (A) and copper-spiked (B) sediments in 1-week (▲ and ▼) and 4-week (■ and ◆) exposures. The fitted curve is survival computed from mortality rates given by equation 3 in the text.

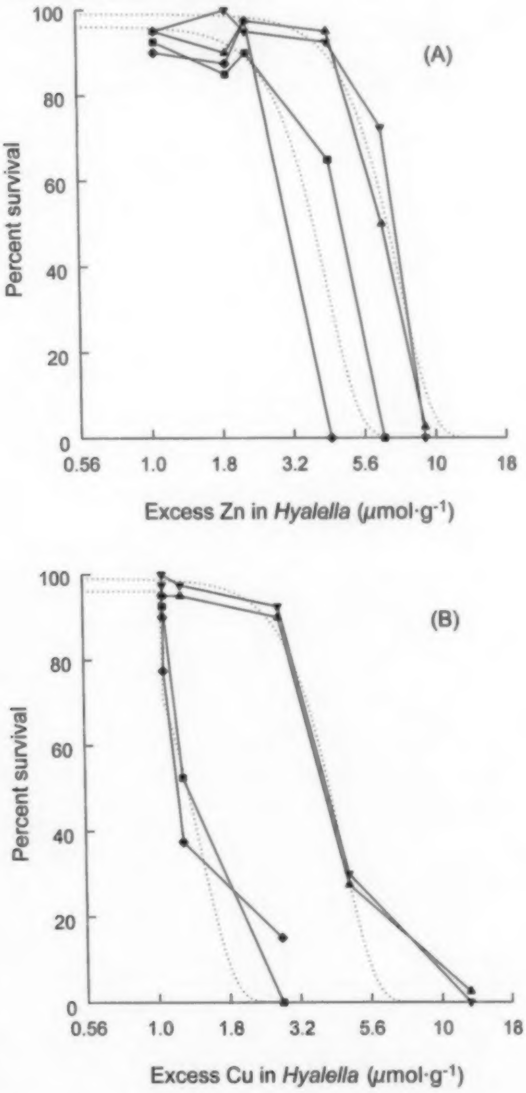
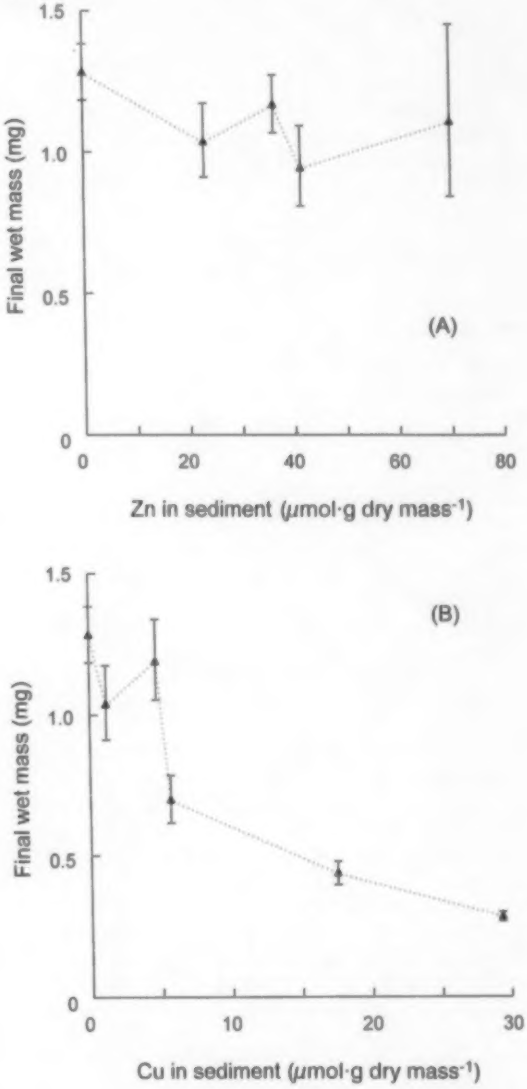


Fig. 4. Mean final wet mass of *Hyalella* exposed to zinc (A) and copper (B) spiked sediments as a function of measured metal concentrations in sediments in 4-week exposures. Vertical bars indicate ± 1 SE.



within the flat portion of the uptake curve. Short term toxicity (1-week LBC25 or 1-week LBC50), however, occurs only at higher copper concentrations in sediments and is associated with a significant increase in body concentration. Because body concentrations of copper in *Hyalella* are elevated at the higher sediment concentrations needed to elicit short term toxicity, but not at the lower sediment concentrations associated with chronic toxicity (<18 µmol/g, Fig. 2B), body concentrations of copper can be used to predict short term, but not chronic copper-induced toxicity. In contrast, both short-term and chronic toxicity of zinc can be predicted from body concentrations of zinc. Short-term and chronic toxicity of copper may, or may not, have different modes of action, depending on whether the discontinuity in the uptake curve (Fig. 2B) is associated only with uptake or also with biological effects.

The sediment concentration at the 4-week LC25, computed using eq. 1 (curves in Fig. 1), is 54 µmol Zn/g and 16 µmol Cu/g. The EC25 for copper for final mass is lower, at 5.2 µmol/g (Table 2). The equivalent water concentrations were computed using the best regression equations for metal in water against metal in sediment and the data in Table 1 ($\log(\mathrm{Zn}_{\mathrm{water}}) = 0.0108 \cdot \mathrm{Zn}_{\mathrm{sed}} - 0.063$ and $\log(\mathrm{Cu}_{\mathrm{water}}) = 0.753 \cdot \log(\mathrm{Cu}_{\mathrm{sed}}) - 0.766$). The water concentrations at the LC25 in the waterborne tests were computed from the LBC25s and the equations for uptake against water concentration provided in Borgmann and Norwood (1995*a*). These values sometimes fall outside the range between the highest no observed effect concentration and the lowest observed effect concentration because the LC25s are based on smoothed regression curves and not the raw data. In either case, the water concentrations tolerated by *Hyalella* in spiked sediment exposures is roughly twice as high as in waterborne toxicity tests (3.29:1.70 for Zn, 0.59:0.33 for Cu, Table 2), possibly because metal complexing agents have leached from the sediments. This increase in metal tolerance on a water concentration basis is not large. Similar studies with cadmium resulted in over a 10-fold increase in aqueous metal tolerated in the presence of sediment (Borgmann et al. 1991).

Discussion

Accumulation of zinc and copper from sediments by *Hyalella* was very different than was accumulation in waterborne exposures. Ignoring, for the moment, the apparent regulation of copper at low sediment copper concentrations, both zinc and copper accumulation increased rapidly with increasing sediment concentrations, showing no sign of levelling off and, if anything, showing an increasing rate of accumulation with increasing sediment concentration. Accumulation of both excess (above background) zinc and excess copper was proportional to the sediment metal concentration raised to an exponent slightly greater than 1 (eqs. 1 and 2). In contrast, excess metal accumulation from water reached saturation at a maximum of 3.55 μmol Zn/g or 3.60 μmol Cu/g (Borgmann and Norwood 1995*a*). No such saturation occurred in spiked sediment exposures (Fig. 2). Background zinc and copper concentrations, however, were similar in both the spiked sediment and waterborne exposure tests (Table 2).

Zinc accumulation from zinc spiked sediments was substantial, even at concentrations well below those causing chronic toxicity (Table 1). Over 3 μmol/g was accumulated above the background of 1.34 μmol/g at the 4-week LBC25. Body concentrations, therefore, can readily be used to infer chronic toxicity. The chronic toxicity threshold on an excess body concentration basis, however, was twice as high as needed to cause the same toxicity in waterborne toxicity tests (Table 2). This is similar to results obtained with cadmium in *Hyalella* (Borgmann et al. 1991). Some of this discrepancy could be due to zinc in the gut. Gut clearance was not performed because of the high depuration rate of zinc (half life 1 day, Borgmann and Norwood 1995*a*). Zinc concentrations in the sediment were, in fact, much higher than zinc concentrations in *Hyalella* (Table 1). If, for the sake of argument, we assume that the true critical body concentration of excess zinc in *Hyalella* is 1.49 μmol/g (water-only experiments, Table 2), that the gut contents have an identical zinc concentration as the sediment (54 μmol/g), and that the rest of the zinc at the LBC25 (3.08 – 1.49 = 1.59 μmol/g) is all in the gut, then the gut contents would contribute 3% of the dry mass of *Hyalella*. This certainly seams feasible. Some, and perhaps all, of the discrepancy in the 4-week LBC25 between waterborne and sediment exposures is, therefore, probably due to gut contents. This could explain why zinc accumulation from spiked sediments does not level off at high exposure concentrations in the way that accumulation from water does; zinc in the gut contents is probably increasing approximately linearly with zinc in the sediment. Unfortunately, the rapid excretion of body zinc (Borgmann and Norwood 1995*a*) makes it impossible to allow time for gut clearance, and separate critical body concentration values must be used for sediment and water-only exposures.

Another process that might be responsible for some of the discrepancy in the 4-week LBC25 between waterborne and sediment exposures is adsorption onto the outside of the exoskeleton. The very small effect of body size on copper or zinc uptake in waterborne exposures suggested that adsorption was minimal in these studies (Borgmann and Norwood 1995*a*). To account for the discrepancy, metal adsorption would have to be much stronger in sediment exposures than in waterborne exposures.

The situation with copper is quite different. The 4-week LBC25 is calculated to occur at 1.05 μmol/g excess Cu (Table 2). This is lower than the critical body concentration for waterborne exposures. However, body copper at this and lower sediment exposures was not dependent on copper in the sediment. Consequently, it is not possible to use body concentrations to infer chronic toxicity. Short-term (1-week) toxicity can, however, be inferred from body concentrations. Unlike zinc, copper caused a reduction in growth, even at concentrations below the 4-week LC25. This has also been observed in copper-contaminated sediments from the field (Kubitz et al. 1995), but not in waterborne exposures (Borgmann et al. 1993). The cause for the reduction in growth, and for the apparent regulation of copper at low sediment concentrations, is not known. One possibility is that copper in sediments inhibits feeding by *Hyalella*, leading to reduced growth. This could also lead to reduced copper uptake from food with increasing copper in the sediment, resulting in an apparent "regulation" of body copper up to the point where this "regulation" breaks down and reduced feeding can no longer control copper uptake. Regardless of whether this mechanism is correct, the reduced growth of *Hyalella* in copper spiked sediments is an important feature for future use in identifying copper toxicity. As indicated above, copper concentrations in *Hyalella* are not reliable indicators of chronic toxicity, but the growth reduction is specific to copper and is not seen in zinc-contaminated sediments (Fig. 4). Reduced growth can, therefore, be used to differentiate between copper and zinc toxicity in sediments and perhaps between copper toxicity and that resulting from other metals as well.

Tolerance of *Hyalella* to copper-contaminated sediments observed in this study was similar to that reported by others, but such comparisons must be made with caution because sediment characteristics can greatly affect metal toxicity. The 10-day LC50 for *Hyalella* exposed to copper spiked sediments from Oregon was 17 μmol/g of sediment (Cairns et al. 1984), close to the 4-week LC25 (Table 2). Suedel et al. (1996) obtained 7- and 14-day LC50s of 3.9 and 5.0 μmole Cu/g using sediments downstream from a copper smelting operation in dilution with clean sediments. Sediments from the Keweenaw Peninsula, Lake Superior, are contaminated from copper tailings and are toxic to *Hyalella*. Mortality, a function of acid volatile sulfide and other factors, was not smoothly related to copper in sediment but exceeded 50% in 10 days at copper concentrations exceeding 5 μmol/g (Ankley et al. 1993). In comparison, the amphipod *Pontoporeia* (= *Diporeia*, Bousfield 1989) was absent from sediments with more that 6.2 µmol Cu/g in Lake Superior along the Keweenaw shore (Kraft 1979). Unfortunately, copper accumulation by amphipods was not reported in these studies.

Simultaneous data on metals in sediments and *Hyalella* and toxicity to *Hyalella* are available for sediments from the Grand Fork River, Montana (Ingersoll et al. 1994, Kemble et al. 1994). Sediments from site CF-01, the most contaminated site and the only site with increased mortality, supported 48% survival of *Hyalella* in 14-day exposures (control survival 74%). Growth was also reduced (length = 2.85 mm) relative to controls (3.89 mm). The only other site with reduced growth was CF-03 (3.22 mm), but survival was high (91%, Kemble et al. 1994). Copper and zinc were 110 and 136 µmol/g, respectively, in CF-01 sediments and would be expected to be toxic if bioavailability in Clark Fork River sediments is similar to that in spiked Hamilton Harbour sediments (Table 1). Highest bioaccumulation (3.78 µmol Cu/g and 3.96 µmol Zn/g) was observed in *Hyalella* exposed to sediments from CF-01 for 28 days, giving an excess above background of 2.66 µmol Cu/g and 3.09 µmol Zn/g (Ingersoll et al. 1994). Metals in control *Hyalella* (1.26 µmol Cu/g, 0.87 µmol Zn/g) were similar to our gauze exposed animals (Table 2). The excess zinc accumulated in CF-01 sediments is equal to that accumulated at the 4-week LBC25 (Table 2), suggesting that zinc in CF-01 sediments is sufficient to contribute to chronic toxicity. The excess copper accumulation is below the 1-week LBC25 (Table 2). Copper accumulation is insufficient, therefore, to imply a strong short-term (1-week) mortality but might still be contributing to chronic toxicity. Furthermore, a growth reduction was observed. Growth was reduced by copper, but not by zinc, in spiked Hamilton Harbour sediments (Fig. 4). This strongly suggests that copper is also contributing to toxicity in CF-01 sediments. In contrast, the cadmium accumulated by CF-01 exposed *Hyalella* was insufficient to cause toxicity (Borgmann et al. 1991), and lead was probably also not toxic, although the latter conclusion is based on exposures of *Hyalella* to waterborne lead only (Borgmann et al. 1993).

Some studies have shown that metal toxicity correlates well with pore water, but not total metal concentrations in sediments (e.g., Ankley et al. 1993). Pore water concentrations were not measured in the present study. Analysis of pore water metal concentrations will help explain variations in metal bioavailability and effects if this variability is due to variations in adsorption of the metal to the solid phase of the sediment. However, some variation in the complexing capacity of pore waters would be expected to occur among different sediments. Consequently, pore water concentrations may not prove to be accurate predictors of toxicity under all circumstances, just as water concentrations are not always reliable predictors of metal toxicity in waterborne exposures (e.g., Borgmann et al. 1991). Comparison of the relative utility of pore water and body concentration measurements would be useful in future studies.

The above is an example of the kind of interpretation possible when metal accumulation is measured in environmental samples and compared with previously determined accumulation: toxicity relationships. This allows a much more reliable prediction of which metals are contributing to toxicity than possible from metal concentrations in water or sediment, where bioavailability is unknown. For metals other than copper, present at concentrations below the toxic threshold, bioaccumulation also allows determination of how close metal availability is to the toxic threshold. Metals accumulated to levels just below those associated with chronic toxicity may not contribute much to toxicity at the time of sample collection, but may do so in the future if the trend is towards increasing metal contamination. This can serve as an early warning indicator, something not possible with toxicity measurements alone. Metal accumulation in *Hyalella* has been used to identify zinc as the metal primarily responsible for toxicity in sediments from Manitouwadge Lake, Ontario. Sediment toxicity in this lake could not be predicted from total metal content in the sediment, but it was predicted from metals accumulated by *Hyalella* when supplemented with data on growth to rule out chronic copper toxicity (Borgmann and Norwood 1997).

Acknowledgement

Wendy Kennette assisted with the bioassays.

References

American Society for Testing and Materials. 1991. Standard guide for conducting sediment toxicity tests with freshwater invertebrates. Standard E1383-90.

Ankley, G.T., and Schubauer-Berigan, M.K. 1995. Background and overview of current sediment toxicity identification evaluation procedures. J. Aquat. Ecosystem Health **4**: 133–149.

Ankley, G.T., Mattson, V.R., Leonard, E.N., West, C.W., and Bennett, J.L. 1993. Predicting the acute toxicity of copper in freshwater sediments: Evaluation of the role of acid-volatile sulfide. Environ. Toxicol. Chem. **12**: 315–320.

Ankley, G.T., Thomas, N.A., Di Toro, D.M., Hansen, D.J., Mahony, J.D., Berry, W.J., Swartz, R.C., Hoke, R.A., Garrison, A.W., Allen, H.E., and Zarba, C.S. 1994. Assessing potential bioavailability of metals in sediments: A proposed approach. Environ. Manage. **18**: 331–337.

Borgmann, U., and Munawar, M. 1989. A new standardized sediment bioassay protocol using the amphipod *Hyalella azteca* (Saussure). Hydrobiologia, **188/189**:425–431.

Borgmann, U., and Norwood, W.P. 1993. Spacial and temporal variability in toxicity of Hamilton Harbour sediments: Evaluation of the *Hyalella azteca* 4 week chronic toxicity test. J. Great Lakes Res. **19**: 72–82.

Borgmann, U., and Norwood, W.P. 1995*a*. Kinetics of excess (above background) copper and zinc in *Hyalella azteca* and their relationship to chronic toxicity. Can. J. Fish. Aquat. Sci. **52**: 864–874.

Borgmann, U., and Norwood, W.P. 1995*b*. EDTA toxicity and background concentrations of copper and zinc in *Hyalella azteca*. Can. J. Fish. Aquat. Sci. **52**: 875–881.

Borgmann, U., and Norwood, W.P. 1997. Identification of the toxic agent in metal-contaminated sediments from Manitouwadge Lake, Ontario, using toxicity–accumulation relationships in *Hyalella azteca*. Can. J. Fish. Aquat. Sci. **54**: 1055-1063.

Borgmann, U., Norwood, W.P., and Babirad, I.M. 1991. Relationship between chronic toxicity and bioaccumulation of cadmium in *Hyalella azteca*. Can J. Fish. Aquat. Sci. **48**:1055–1060.

Borgmann, U., Norwood, W.P., and Clarke, C. 1993. Accumulation, regulation and toxicity of copper, zinc, lead and mercury in *Hyalella azteca*. Hydrobiologia, **259**: 79–89.

Borgmann, U., Ralph, K.M., and Norwood, W.P. 1989. Toxicity test procedures for *Hyalella azteca*, and chronic toxicity of cadmium and pentachlorophenol to *H. azteca*, *Gammarus fasciatus*, and *Daphnia magna*. Arch. Environ. Contam. Toxicol. **18**: 756–764.

Bousfield, E.L. 1958. Fresh-water amphipod crustaceans of glaciated North America. Canadian Field-Naturalist **72**: 55–113.

Bousfield, E.L. 1989. Revised morphological relationships within the amphipod genera *Pontoporeia* and *Gammaracanthus* and the "glacial relic" significance of their postglacial distributions. Can. J. Fish. Aquat. Sci. **46**: 1714–1725.

Cairns, M.A., Nebeker, A.V., Gakstatter, J.H., and Griffis, W.L. 1984. Toxicity of copper-spiked sediments to freshwater invertebrates. Environ. Toxicol. Chem. **3**: 435–445.

Connolly, J.P. 1985. Predicting single-species toxicity in natural water systems. Environ. Toxicol. Chem. **4**: 573–582.

Ingersoll, C.G., and Nelson, M.K. 1990. Testing sediment toxicity with *Hyalella azteca* (Amphipoda) and *Chironomus riparius* (Diptera). *In* Aquatic Toxicology and Risk Assessment: Thirteenth Volume, ASTM STP 1096, *Edited by* W.G. Landis and W.H. van der Schalie, American Society for Testing and Materials, Philadelphia. pp. 93–109.

Ingersoll, C.G., Brumbaugh, W.G., Dwyer, F.J., and Kemble, N.E. 1994. Bioaccumulation of metals by *Hyalella azteca* exposed to contaminated sediments from the upper Clark Fork River, Montana. Environ. Toxicol. Chem. **13**: 2013–2020.

Ingersoll, C.G., Ankley, G.T., Benoit, D.A., Brunson, E.L., Burton, G.A., Dwyer, F.J., Hoke, R.A., Landrum, P.F., Norberg-King, T.J., and Winger, P.V. 1995. Toxicity and bioaccumulation of sediment-associated contaminants using freshwater invertebrates: A review of methods and applications. Environ. Toxicol. Chem. **14**: 1885–1894.

Kemble, N.E., Brumbaugh, W.G., Brunson, E.L., Dwyer, F.J., Ingersoll, C.G., Monda, D.P., and Woodward, D.F. 1994. Toxicity of metal-contaminated sediments from the upper Clark Fork River, Montana, to aquatic invertebrates and fish in laboratory exposures. Environ. Toxicol. Chem. **13**: 1985–1997.

Kraft, K.J. 1979. *Pontoporeia* distribution along the Keweenaw shore of Lake Superior affected by copper tailings. J. Great Lakes Res. **5**: 28–35.

Krantzberg, G. 1994. Spatial and temporal variability in metal bioavailability and toxicity of sediment from Hamilton Harbour, Lake Ontario. Environ. Toxicol. Chem. **13**: 1685–1698.

Kubitz, J.A. Lewek, E.C., Besser, J.M., Drake III, J.B., and Giesy, J.P. 1995. Effects of copper-contaminated sediments on *Hyalella azteca*, *Daphnia magna*, and *Ceriodaphnia dubia*: Survival, growth and enzyme inhibition. Arch. Environ. Contam. Toxicol. **29**: 97–103.

Landrum, P.F., Lee II, H., and Lydy, M.J. 1992. Toxicokinetics in aquatic systems: Model comparisons and use in hazard assessment. Environ. Toxicol. Chem. **11**: 1709–1725.

Luoma, S.N. 1989. Can we determine the biological availability of sediment-bound trace elements? Hydrobiologia, **176/177**: 379–396.

McCarty, L.S., and Mackay, D. 1993. Enhancing ecotoxicological modeling and assessment: Body residues and modes of toxic action. Environ. Sci. Technol. **27**: 1719–1728.

Saouter, E., Hare, L., Campbell, P.G.C., Boudou, A., and Ribeyre, F. 1993. Mercury accumulation in the burrowing mayfly *Hexagenia rigida* (Ephemeroptera) exposed to CH3HgCl or HgCl2 in water and sediment. War. Res. **27**: 1041–1048.

Schubauer-Berigan, M.K., Amato, J.R., Ankley, G.T., Baker, S.E., Burkhard, L.P., Dierkes, J.R., Jenson, J.J., Lukasewycz, M.T., and Norberg-King, T.J. 1993. The behaviour and identification of toxic metals in complex mixtures: Examples from effluent and sediment pore water toxicity identification evaluations. Arch. Environ. Contam. Toxicol. **24**: 298–306.

Stephenson, M., and Mackie, G.L. 1988. Multivariate analysis of correlations between environmental parameters and cadmium concentrations in *Hyalella azteca* (Crustacea: Amphipoda) from central Ontario lakes. Can. J. Fish. Aquat. Sci. **45**: 1705–1710.

Suedel, B.C., Deaver, E., and Rodgers, J.H., Jr. 1996. Experimental factors that may affect toxicity of aqueous and sediment-bound copper to freshwater organisms. Arch. Environ. Contam. Toxicol. **30**: 40–46.

Identification of the toxic agent in metal-contaminated sediments from Manitouwadge Lake, Ontario, using toxicity–accumulation relationships in *Hyalella azteca*

Uwe Borgmann and Warren P. Norwood

Abstract: Toxicity of sediments from Manitouwadge Lake, Ontario, to *Hyalella* correlated closely with bioaccumulation of zinc but not copper. Bioaccumulation in 1-week exposures was sufficient to infer chronic zinc toxicity. Close similarity between toxicity–accumulation relationships from Manitouwadge Lake and those obtained from zinc-spiked Hamilton Harbour sediments indicate that toxicity is due to zinc itself and not some other chemical that correlates with zinc in sediments. Sediment concentrations of zinc, on the other hand, are unreliable indicators of effects; toxicity was not highest in sediments from the most contaminated site. Copper accumulation was insufficient to cause short-term (1-week) toxicity. Chronic copper toxicity cannot be predicted from bioaccumulation, but the absence of a significant growth reduction, which is specific to copper, strongly suggests that the contribution of copper to chronic toxicity was minimal. Body concentrations of zinc and copper in wild animals from contaminated lakes (in contrast to laboratory animals exposed to sediments from those lakes) are not reliable indicators of metal toxicity, either because these amphipods have adapted to contaminated conditions or because they survive in selected microhabitats with reduced metal availability.

Résumé : La toxicité des sédiments du lac Manitouwadge, Ontario, pour *Hyalella* était en étroite corrélation avec la bioaccumulation du zinc, mais non de celle du cuivre. La bioaccumulation consécutive à des expositions d'une semaine était suffisante pour déduire une toxicité chronique du zinc. Une étroite similitude entre les relations toxicité–accumulation obtenues dans le lac Manitouwadge et celles obtenues à partir des sédiments dopés par le zinc du port de Hamilton indique que la toxicité est attribuable au zinc lui-même et non à un quelconque autre produit chimique en corrélation avec le zinc dans les sédiments. Par ailleurs, les concentrations de zinc dans les sédiments sont des indicateurs peu fiables des effets; la toxicité n'était pas la plus élevée dans les sédiments provenant du site le plus contaminé. L'accumulation de cuivre était insuffisante pour causer une toxicité à court terme (1 semaine). On ne peut prévoir la toxicité chronique du cuivre à partir de la bioaccumulation, mais l'absence d'une réduction substantielle de la croissance, qui est spécifique du cuivre, laisse fortement entendre que la contribution du cuivre à la toxicité chronique était minimale. Les concentrations corporelles de zinc et de cuivre chez les animaux sauvages vivant dans les lacs contaminés (contrairement aux animaux de laboratoire exposés à des sédiments provenant de ces lacs) ne sont pas des indicateurs fiables de la toxicité par les métaux, soit parce que les amphipodes se sont adaptés à la contamination soit parce qu'ils survivent dans des micro habitats choisis où la disponibilité des métaux est réduite.
[Traduit par la Rédaction]

Introduction

Manitouwadge Lake, north of Lake Superior in Ontario, is contaminated with zinc and copper from mining activities. Detailed studies on the white sucker (*Catostomus commersoni*) population demonstrated impaired reproduction owing to severely reduced growth rates in female fish after reaching reproductive maturity (Munkittrick and Dixon 1988). This has been attributed to a poor food supply resulting from the virtual absence of large benthic invertebrates such as amphipods and mayflies rather than from a direct effect of metals on fish (Munkittrick et al. 1991). The effect of mining on the aquatic ecosystem appears, therefore, to be largely through toxic effects on sensitive benthic invertebrates. It is not clear, however, whether zinc, copper, or both metals are contributing to toxicity or if other chemicals associated with mining are also involved.

Identification of the agent(s) responsible for toxicity is a common problem in assessment of environmental samples. The concentration of total metals in sediments is not a reliable indicator of biological effects, because this does not take metal bioavailability into account (Luoma 1989; Ankley et al. 1994). Body concentrations are likely to be more reliable predictors of toxicity (Borgmann et al. 1991). Borgmann and Norwood (1997) determined the relationship between zinc and copper accumulation and toxicity from spiked Hamilton Harbour sediments in the amphipod *Hyalella azteca* for use in toxic

Received April 18, 1996. Accepted October 7, 1996.
J13425

U. Borgmann[1,2] and W.P. Norwood.[1] Department of Fisheries and Oceans, Great Lakes Laboratory for Fisheries and Aquatic Sciences, Burlington, ON L7R 4A6, Canada.

[1] Present address for both authors: National Water Research Institute, Environment Canada, Burlington, ON L7R 4A6, Canada.

[2] Author to whom all correspondence should be addressed. e-mail: uwe.borgmann@cciw.ca

Table 1. Major ions (mM), DOC (mg/L), and pH of Lake Ontario (tap) water (mean and range) and Loken and Manitouwadge Lake water initially and at the end of the 1- and 4-week experiments.

		Loken Lake water			Manitouwadge Lake water		
Ion	Tap water, initial	Initial	1 week	4 weeks	Initial	1 week	4 weeks
Ca^{2+}	0.96 (0.94–1.02)	0.68	0.60 (0.51–0.66)	0.73 (0.66–0.85)	0.81	1.22 (0.77–1.42)	1.90 (0.85–2.74)
Mg^{2+}	0.35 (0.34–0.38)	0.23	0.22 (0.19–0.23)	0.26 (0.23–0.32)	0.27	0.51 (0.27–0.72)	0.91 (0.29–1.23)
Na^+	0.570 (0.522–0.648)	0.036	0.074 (0.065–0.100)	0.106 (0.074–0.138)	0.133	0.167 (0.155–0.177)	0.223 (0.176–0.253)
K^+	0.045 (0.038–0.061)	0.016	0.047 (0.036–0.065)	0.057 (0.046–0.079)	0.026	0.063 (0.055–0.067)	0.078 (0.066–0.091)
HCO_3^-	1.83 (1.75–1.91)	1.76	1.74 (1.54–1.87)	1.61 (1.43–1.82)	1.31	0.86 (0.53–1.49)	0.72 (0.18–1.60)
Cl^-	0.721 (0.657–0.776)	0.023	0.071 (0.066–0.083)	0.102 (0.075–0.130)	0.137	0.170 (0.161–0.175)	0.219 (0.186–0.247)
SO_4^{2-}	0.344 (0.320–0.392)	0.036	0.074 (0.051–0.095)	0.139 (0.051–0.183)	0.445	1.432 (0.440–1.905)	2.687 (0.503–4.133)
NH_4^+	—	≤0.04	≤0.39	<0.03	<0.03	≤0.29	<0.02
DOC	2.0 (0.9–2.9)	9.3	10.5 (9.9–11.6)	13.0 (10.6–14.2)	11.6	9.7 (6.6–16.9)	7.4 (5.3–9.8)
pH	8.52 (8.45–8.58)	8.55	8.12 (7.84–8.38)	8.20 (7.75–8.85)	8.46	7.64 (7.14–8.00)	7.76 (6.87–8.29)

metal identification in environmental samples. These relationships should be useful for identifying either zinc or copper toxicity in 1-week exposures or zinc toxicity in chronic exposures; copper toxicity in chronic exposures cannot, however, be inferred from body concentrations because body concentrations are independent of exposure at low copper concentrations in sediments. Inhibition of growth, however, occurs only with copper, and this should help identify chronic copper toxicity, if it occurs (Borgmann and Norwood 1997). The purpose of this study was to determine zinc and copper uptake and toxicity in 1- and 4-week exposures to sediments from Manitouwadge Lake and a reference (Loken) lake for comparison with accumulation–toxicity relationships from spiked Hamilton Harbour sediments. Specifically, we wished to determine if we could identify the metal responsible for toxicity, if 1-week exposures were sufficient to predict chronic toxicity of zinc, and if measurement of growth rate could help quantify the contribution of copper to chronic toxicity. In addition, wild *Hyalella* were collected from the reference lake for comparative 1-week metal accumulation measurements, and metals were also measured in freshly caught wild animals from both lakes.

Methods

A map of the study area is shown in Munkittrick and Dixon (1988). Sediments were collected from three sites (M1, M2, and M3) in contaminated Manitouwadge Lake and three sites in uncontaminated Loken Lake (L1, L2, and L3) at depths of 0.5–2 m with an Eckman sampler on September 23–25, 1994. Site M1 was close to the entrance of Fox Creek, which received drainage from mine tailings; site M3 was on the southeast corner of Manitouwadge Lake, just west of the outflow to Little Manitouwadge Lake (2 km from M1); and site M2 was between M1 and M3 on the eastern shore of Manitouwadge Lake, about three times further away from M1 than M3. Sites L1, L2, and L3 were all in the northeast corner of Loken Lake, about 50 m apart. Many *Hyalella* were observed on the surface of all Loken Lake sediments but none on the surface of M1 or M2 sediments, and only one amphipod was collected from the Eckman grab at site M3. Although much less abundant than in Loken Lake, it was possible to collect *Hyalella* in the vicinity of sites M1–M3 using a small dredge pulled through the weeds near shore. These, and amphipods from L1, were dried immediately and saved for later analysis (the M1 sample was accidentally spilled and lost). In addition, sufficient live *Hyalella* were collected by dredge in the vicinity of sites L1–L3 and returned live to the laboratory for a few toxicity tests. Water from Loken and Manitouwadge lakes was collected in 10-L polypropylene carboys from the surface away from shore in the area of the sampling sites.

Amphipods were cultured as described in Borgmann and Norwood (1997) using Burlington city tap water originating from Lake Ontario. Toxicity tests were conducted from October to December 1994 as described in Borgmann and Norwood (1997) using 40 mL of sediment plus 160 mL of water in 250-mL beakers aerated throughout the experiments. Twenty 0- to 1-week-old amphipods were added to each beaker for chronic (4-week) tests, and twenty 4- to 5-week-old amphipods were added for 1-week tests. Eight experiments were conducted: four chronic and four 1-week tests. Half of the experiments were conducted using tap (Lake Ontario) water and half were conducted using water from the same lake as the sediments. Each experiment contained two replicate beakers with sediment from each site and was repeated a second time, giving four replicate estimates of survival and growth for each site and overlying water combination (there was no significant difference in survival between experiments, $P > 0.1$, ANOVA). Controls containing cotton gauze instead of sediment were run during each experiment. During experiments with field water, two sets of controls were run: one using water from Loken Lake and a second set using water from Manitouwadge Lake. A ninth experiment was conducted 1 year later (December 1995) to verify survival in 4-week chronic exposures. The water was not changed throughout the incubation period, but evaporated water was replaced with double distilled water, as required. Amphipods were fed 5 mg of Tetra-Min fish food flakes three times each week. Surviving amphipods, as well as sediment subsamples, were dried and analyzed for zinc and copper as described in Borgmann and Norwood (1997).

The hardness (Ca^{2+} and Mg^{2+}), alkalinity (HCO_3^-), and pH in Loken and Manitouwadge Lake water were similar to that of Lake Ontario (tap) water (Table 1). Sodium, however, was considerably lower, especially in Loken Lake water. This is of some concern because *Hyalella* has an absolute requirement for sodium (Borgmann 1996). Chloride was also lower in both lakes, as was sulphate in Loken Lake water, but neither of these ions is required by *Hyalella*. Some leaching of ions from sediments to water appeared to occur. This was relatively minor for most ions except for sulphate in Manitouwadge Lake, which reached concentrations of up to 4.1 mM (Table 1). *Hyalella* from our laboratory can, however, tolerate $MgSO_4$ to at least 5.6 mM with no noticeable mortality in 4-week exposures (U. Borgmann, unpublished data). Ammonia concentrations (Table 1) were at detection limits (0.1 mM) or below the 4-week LC50 of 1 mM in Lake Ontario water (Borgmann 1994).

Statistical analyses were performed by ANOVA using SYSTAT 5.0. All metal concentration data were logarithmically transformed, and survival data were converted to mortality rates (log(survival)/time) and then log transformed, before statistical analysis to equalize variances.

Predicted mortality rates based on previously determined relationships between survival and metal accumulation were computed using:

$$[1] \quad m = m' + m'' = m' + a(C_{TB} - C_{Bk})^n$$

Table 2. Density, moisture content, organic matter (estimated as loss on ignition, LOI), and metal concentrations (range, $n = 4$) measured in sediments.

				Zinc concentration				Copper concentration			
Site	Density, g /m L	Percent moisture	Percent LOI	μmol/g dry wt.	μmol/g LOI	μmol/g wet wt.	μmol/mL	μmol/g dry wt.	μmol/g LOI	μmol/g wet wt.	μmol/ mL
L1	1.09	82.4	19.6	1.8 (0.4–13.4)	9.3	0.32	0.35	0.32 (0.18–0.51)	1.6	0.056	0.061
L2	1.17	70.3	12.7	1.6 (0.5–5.3)	13	0.48	0.57	0.16 (0.13–0.20)	1.2	0.047	0.055
L3	1.19	67.3	8.6	1.4 (0.5–5.8)	16	0.45	0.54	0.22 (0.10–0.47)	2.5	0.071	0.084
M1	1.09	84.7	16.3	139 (131–156)	855	21	23	31.9 (30.3–33.9)	196	4.9	5.3
M2	1.23	66.9	8.4	64 (42–112)	755	21	26	7.1 (5.7–11.9)	85	2.4	2.9
M3	1.20	69.9	11.8	49 (42–60)	417	15	18	10.1 (8.4–11.8)	85	3.0	3.6

Table 3. Geometric mean concentration (with range given in parentheses) of zinc and copper measured in water at the end of 1- and 4-week exposures to cotton gauze in Lake Ontario (GO), Loken Lake (GL), and Manitouwadge Lake (GM) water, and to sediments from the six sites.

	Zinc (μM)		Copper (μM)	
Site	1 week	4 weeks	1 week	4 weeks
GO	0.068 (0.007–0.294)	0.038 (0.004–0.147)	0.022 (0.011–0.062)	0.027 (0.015–0.048)
GL	0.181 (0.070–0.690)	0.069 (0.021–0.373)	0.141 (0.075–0.478)	0.063 (0.017–0.211)
GM	1.023 (0.635–2.441)	0.618 (0.204–1.999)	0.183 (0.108–0.309)	0.097 (0.016–0.269)
L1	0.033 (0.008–0.213)	0.048 (0.013–0.173)	0.020 (0.003–0.241)	0.020 (0.003–0.250)
L2	0.048 (0.005–0.135)	0.026 (0.002–0.162)	0.014 (0.001–0.057)	0.018 (0.002–0.349)
L3	0.040 (0.008–0.419)	0.055 (0.010–0.172)	0.014 (0.002–0.060)	0.012 (0.002–0.062)
M1	14.1 (7.0–33.5)	7.1 (1.6–22.9)	0.300 (0.064–1.157)	0.230 (0.078–1.022)
M2	24.2 (10.0–66.4)	14.3 (1.6–45.5)	0.090 (0.017–0.430)	0.097 (0.007–0.334)
M3	7.1 (0.6–22.8)	4.4 (0.7–15.5)	0.078 (0.011–0.291)	0.086 (0.011–0.283)

[2] Percent survival = $100\exp(-mt)$

where m is the total instantaneous mortality rate (week^{-1}), m' is the control mortality rate (computed from survival of controls exposed to cotton gauze in tap water), m'' is the toxicant induced mortality rate, a and n are constants, and t is exposure time in weeks (Borgmann and Norwood 1997). C_{TB} is the total body metal concentration and C_{Bk} is the background metal concentration (cotton gauze control with tap water). The value of n was set at 4 and a was set equal to 0.0003 and 0.0008 for Zn in the 1- and 4-week sediment exposures, and 0.0025 and 0.06 for Cu in the 1- and 4-week exposures, respectively (Borgmann and Norwood 1997).

Results

Sediments from Manitouwadge Lake were heavily contaminated with zinc and copper while those from Loken Lake were quite clean (Table 2), confirming previous measurements (Munkittrick et al. 1991). Site M1, closest to the mine tailings, contained much higher metal concentrations than did M2 or M3 on a dry mass basis. Sediments from this site also had a higher organic and water content and a lower density; on a volume basis metal content was similar at all three sites within each lake.

Water from Manitouwadge Lake contained substantially higher zinc concentrations than tap water or water from Loken Lake (gauze exposures; Table 3). Copper was similar in Loken and Manitouwadge Lake waters, but higher than in tap water. Zinc and copper in overlying water were low and similar to tap water in gauze controls at the end of 1- and 4-week sediment exposures with Loken Lake sediments. Substantial amounts of zinc leached from the sediments of Manitouwadge Lake, however, especially from site M2 (Table 3). A lesser amount of copper leached from Manitouwadge sediments, with highest amounts leaching from site M1 sediments.

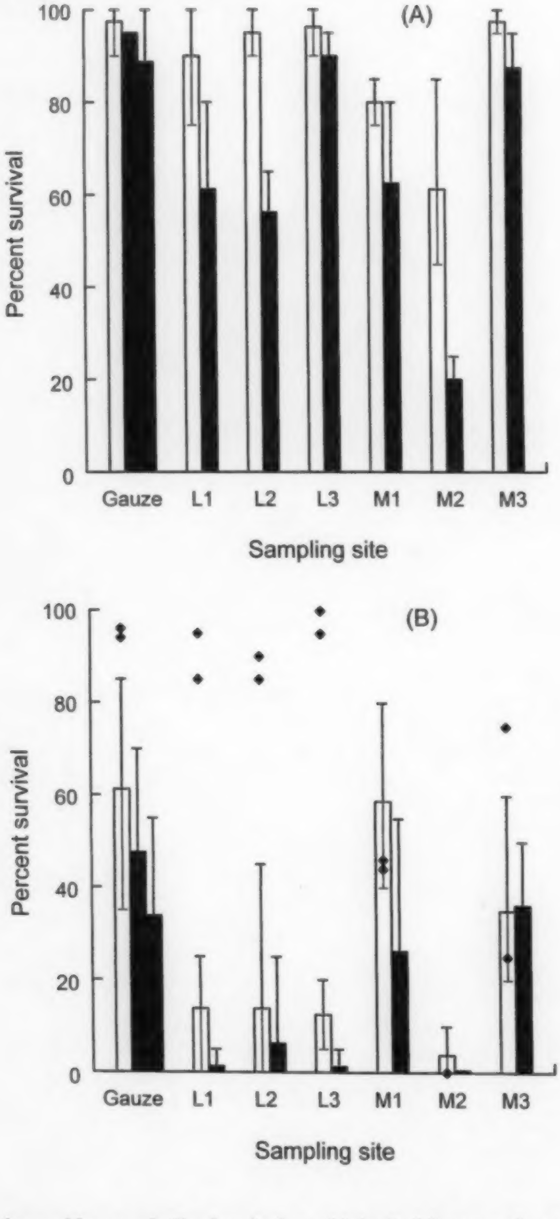
Survival

Exposures of *Hyalella* to sediments were done using both Lake Ontario (tap) water and water from the same lake as sediments were collected. Ideally, a true assessment of the toxicity of an environmental sample should involve exposure of animals to both sediments and water from the same site. However, collection of sufficient water is usually impractical. Exposures were, therefore, conducted using both field and laboratory water to determine if results using laboratory water were similar to those obtained using water from the field.

Highest mortality in 1-week exposures occurred to *Hyalella* exposed to site M2 sediments (Fig. 1A). Mortality rates in this sediment were greater than at all other sites except M1 (ANOVA, Tukey test, $P < 0.01$). Significant mortality also occurred at sites L1, L2, and M1, and mortality was greater when site water was used instead of tap water (ANOVA, $P < 0.01$).

Unexplained mortality occurred in the gauze controls during the 4-week chronic exposures, making data interpretation difficult. Chronic mortality in M1 and M3 sediments was not significantly different from the gauze controls (Fig. 1B). Mortality in M2 sediments was severe, but mortality in Loken Lake sediments was unexpectedly high. A single repeat experiment with 2 replicates/site, conducted 1 year later with tap water only, had good survival in cotton gauze and all Loken Lake sediments. The unexplained toxic factor in Loken Lake sediments disappeared during sediment storage. This might have

Fig. 1. Mean survival of *Hyalella azteca* exposed to cotton gauze or sediments from Loken (L1, L2, L3) or Manitouwadge (M1, M2, M3) Lake for 1 (A) or 4 weeks (B) with either Lake Ontario tap (open bars) or site (solid bars) water. Gauze controls were exposed to Lake Ontario (left), Loken Lake (centre), and Manitouwadge Lake (right) water. Bars indicate minimum and maximum range ($n = 4$). Diamonds indicate results from experiments repeated after 1 year using stored sediments.



been either a volatile chemical or a biological factor such as a parasite. The high toxicity of M2 sediments (0% survival) was, however confirmed. Site M1 and M3 sediments had similar toxicity in the repeat experiment, but this was now much lower than that of controls and Loken Lake sediments (Fig. 1B). Despite uncertainties surrounding the low control survival initially and the effects of sediment storage, it is clear that site M2 sediments are extremely toxic during chronic exposures. Site M1 and M3 sediments might also show some chronic toxicity.

Metal accumulation

Unlike survival, metal accumulation by *Hyalella* from sediments was relatively independent of both exposure time (1- vs. 4-week) and the source of the overlying water. Substantial zinc accumulation occurred from all Manitouwadge sediments, but accumulation was highest from site M2 sediments (Figs. 2A and 2B). Significant accumulation of copper also occurred from all Manitouwadge sediments, but there were no consistent site to site differences within the lake (Figs. 2C and 2D). Zinc accumulation, therefore, correlated with toxicity (Fig. 1), but copper accumulation did not. There was no accumulation of either zinc or copper from Loken Lake sediments (Fig. 2).

Toxicity – metal accumulation relationships

The relationship between survival and zinc accumulation matched closely with the survival–accumulation relationship obtained for *Hyalella* exposed to spiked Hamilton Harbour sediments (Fig. 3). Data points fit either close to the spiked sediment curve, implying zinc-induced toxicity, or fell below the curve, indicating toxicity due to other factors. Additional data points at 0% survival and >7 μmol Zn/g belong on the chronic toxicity curve (Fig. 3B), but the lack of survivors in site M2 sediments precluded body concentration analysis. The close fit of survival to body concentration in the Manitouwadge and spiked Hamilton Harbour sediment exposures strongly suggests that toxicity is, in fact, due to zinc and not due to some other agent that correlates with zinc concentrations in Manitouwadge sediments.

The clear relationship between toxicity and zinc accumulation was not mirrored in a toxicity – sediment concentration relationship (Fig. 4). Highest mortality (site M2) in both 1- and 4-week exposures occurred at sediment concentrations lower than those causing similar toxicity in spiked Hamilton Harbour sediments. Furthermore, sediments with the highest zinc concentrations (M1) were much less toxic than spiked Hamilton Harbour sediments with equivalent zinc concentrations (Fig. 4). Clearly, total zinc concentration in sediments is an unreliable indicator of toxicity. Some, but not all, of this discrepancy may be due to the organic content of the sediment. However, after normalization to organic matter, zinc in M1 sediment is still slightly higher than in M2 sediment (Table 2). Zinc on a volume basis is slightly higher in M2 than M1 sediments, but this hardly seems enough to account for the much higher toxicity of M2 sediments. Body concentrations are, therefore, much better predictors of zinc toxicity than sediment concentrations.

In contrast to the zinc data, toxicity did not match copper accumulation. Highest mortality in the 1-week exposures occurred at a body concentration well below the survival – copper accumulation relationship obtained in copper-spiked Hamilton Harbour sediments (Fig. 5A), indicating that something other than copper (i.e., zinc) was responsible for mortality. The 4-week exposure data are much less clear. Copper concentrations in *Hyalella* exposed to Manitouwadge sediments were high enough that they could have contributed to

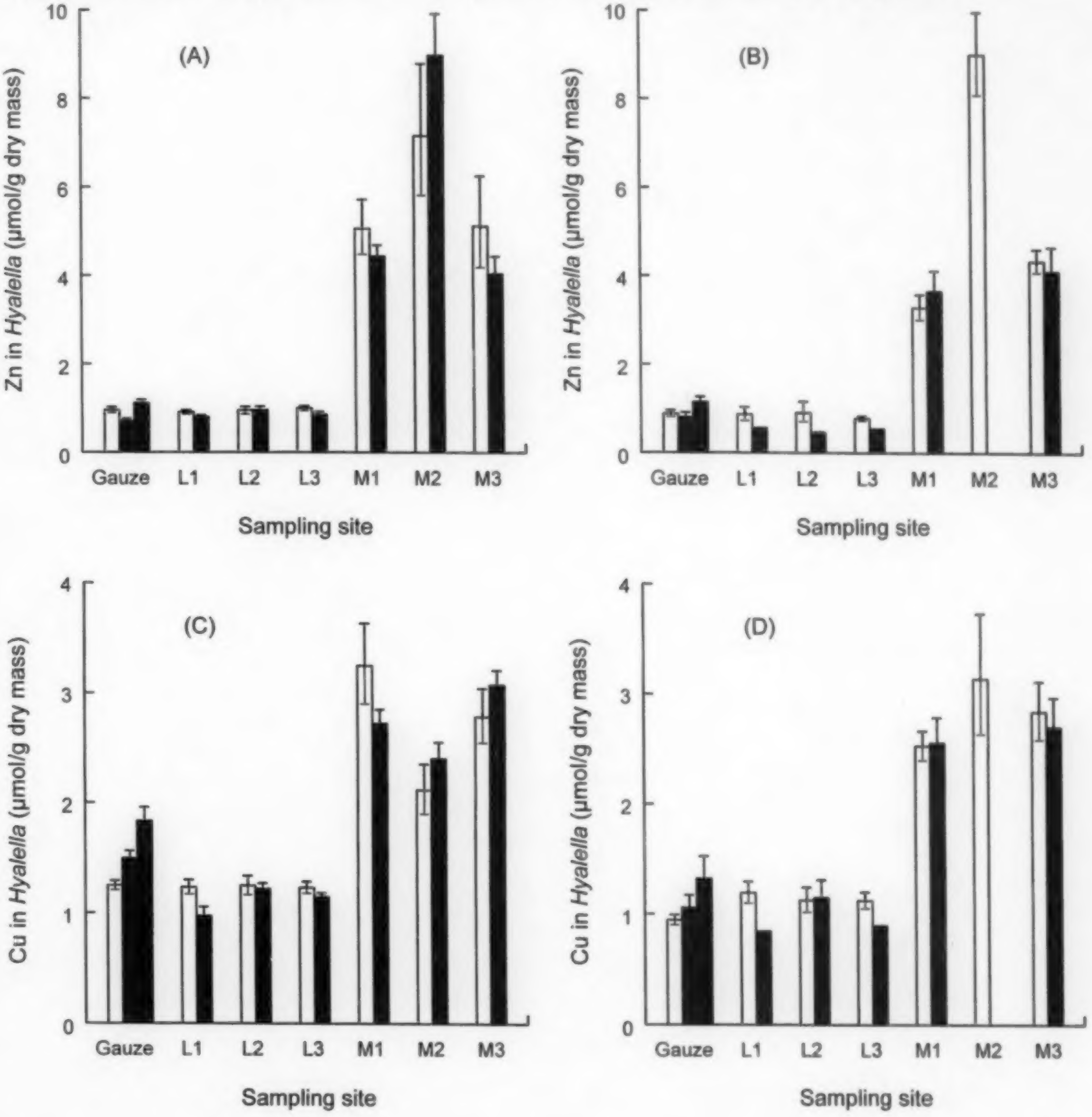


Fig. 2. Mean accumulation (± SE) of zinc (A and B) and copper (C and D) by *Hyalella* exposed to cotton gauze or sediments from Loken (L1, L2, L3) or Manitouwadge (M1, M2, M3) Lake for 1 (A and C) or 4 weeks (B and D) with either Lake Ontario tap (open bars) or site (solid bars) water. Gauze controls were exposed to Lake Ontario (left), Loken Lake (centre), and Manitouwadge Lake (right) water.

chronic copper toxicity. The 4-week LC25 for copper occurred at an excess body copper concentration of 1.05 µmol/g in spiked sediments (Borgmann and Norwood 1997). When added to the background concentration in control animals (0.94 µmol/g in 4-week experiments, Fig. 2D), some chronic toxicity might be expected above 2 µmol Cu/g. However, at sediment copper concentrations resulting in 25% mortality and below in 4 weeks, copper accumulation in *Hyalella* is independent of copper in sediment; completely nontoxic sediments result in similar levels of copper accumulation (Borgmann and Norwood 1997). Although copper is clearly not responsible for the 1-week toxicity, it is not clear from bioaccumulation data whether copper is contributing to chronic mortality.

Unlike zinc, copper in sediments caused a reduction in growth rates in *Hyalella* at concentrations below those causing chronic mortality, and this can be used to differentiate between chronic zinc and copper toxicity (Borgmann and Norwood 1997. Although somewhat variable, there was no clear evidence of a reduction in growth rate (Fig. 6). Growth, relative to gauze controls, was enhanced in site L1, L2, and M3 sediments,

Fig. 3. Mean survival of *Hyalella* exposed to cotton gauze or sediments from Loken or Manitouwadge Lake for 1 (A) or 4 weeks (B) with either Lake Ontario tap (■) or site (◆) water as a function of total body zinc concentration. The curve was computed from eqs. 1 and 2 in the text using control mortality and background zinc concentrations from gauze controls exposed to Lake Ontario water, and $a = 0.0003$ at 1 week and 0.0008 at 4 weeks as obtained in spiked Hamilton Harbour sediments (Borgmann and Norwood 1996).

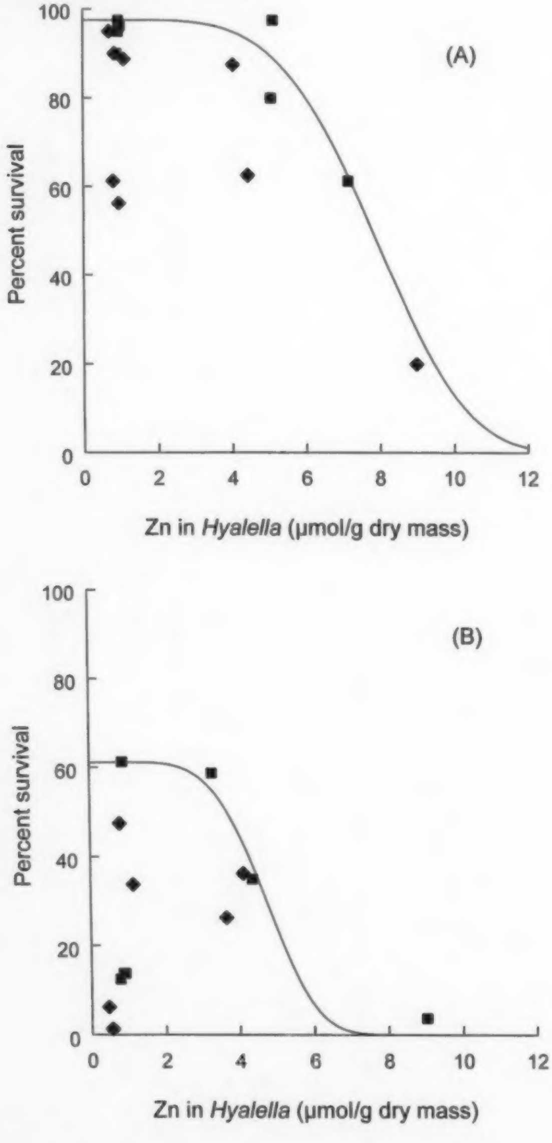
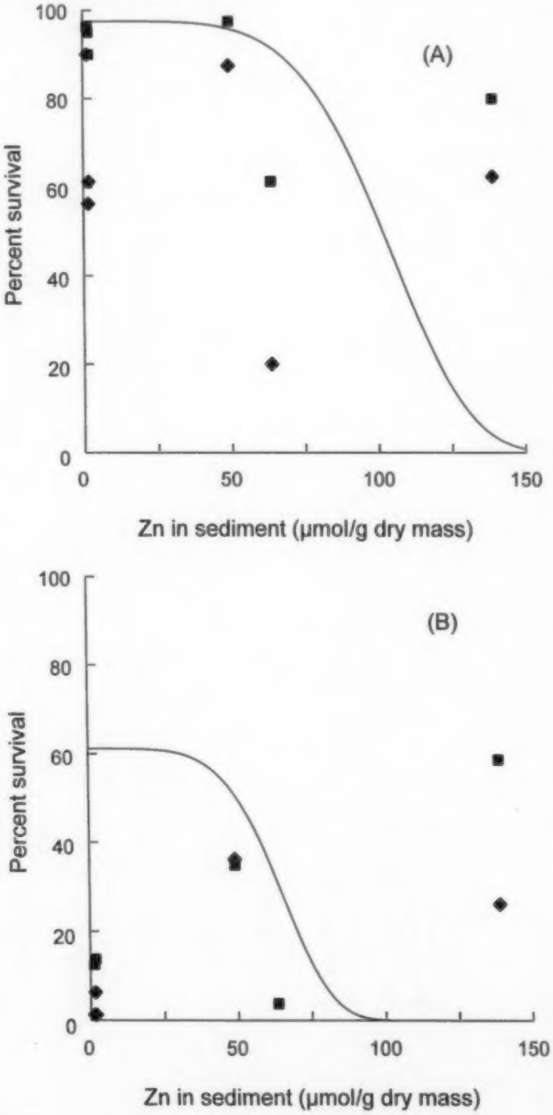


Fig. 4. Mean survival of *Hyalella* exposed to cotton gauze or sediments from Loken or Manitouwadge Lake for 1 (A) or 4 weeks (B) with either Lake Ontario tap (■) or site (◆) water as a functional of total sediment zinc concentration. The curve was obtained using spiked Hamilton Harbour sediments(Borgmann and Norwood 1996) corrected for control mortality from gauze controls exposed to Lake Ontario water.

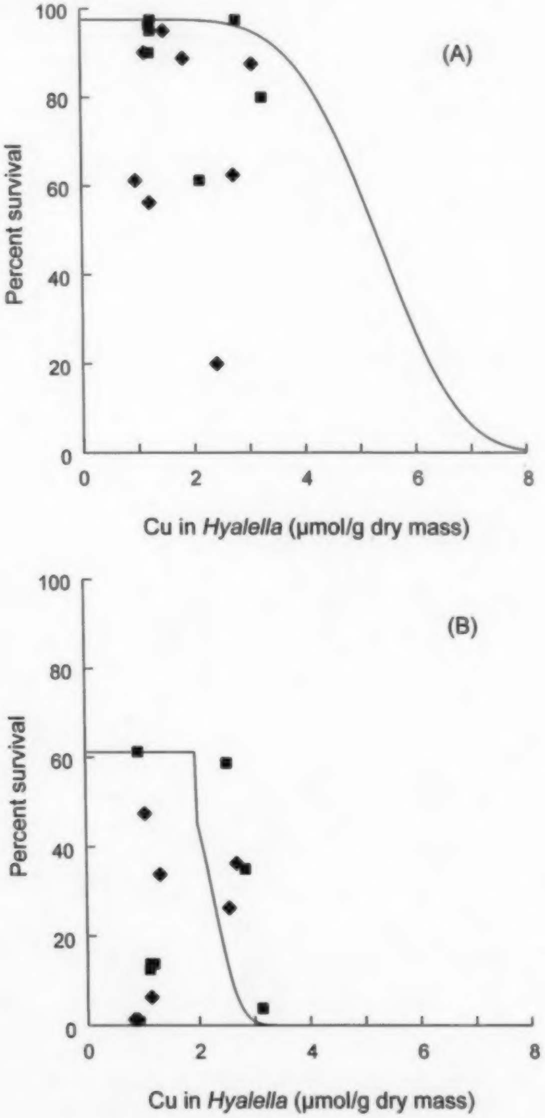


suggesting the presence of nutritionally beneficial agents. Mean body size at week 4 was not, however, markedly reduced in any sediments except in one case based on a single replicate with survivors. By comparison, in copper-spiked sediments, final body size deceased from 1.28 mg in gauze controls, to 1.03 mg in nonspiked sediments (91% survival), to 0.69 mg at 78% survival, and to 0.44 mg at 45% survival (Borgmann and Norwood 1997). Final body size in Manitouwadge sediments was clearly greater than 50% of gauze controls, suggesting it is very unlikely that the high mortality in M2 sediments is related to copper toxicity.

Comparison of laboratory and wild amphipods

Sufficient *Hyalella* were collected from Loken Lake to allow

Fig. 5. Mean survival of *Hyalella* exposed to cotton gauze or sediments from Loken or Manitouwadge Lake for 1 (A) or 4 weeks (B) with either Lake Ontario tap (■) or site (◆) water as a function of total body copper concentration. The curve was computed from eqs. 1 and 2 in the text using control mortality and background copper concentrations from gauze controls exposed to Lake Ontario water, and $a = 0.0025$ at 1 week, $a = 0.06$ at 4 weeks if $\mathrm{Cu}_{\mathrm{TB}} - \mathrm{Cu}_{\mathrm{Bk}} > 1.05$, and $a = 0$ at 4 weeks if $\mathrm{Cu}_{\mathrm{TB}} - \mathrm{Cu}_{\mathrm{Bk}} < 1.05$, as obtained in spiked Hamilton Harbour sediments (Borgmann and Norwood 1996).



a single experiment exposing them to gauze and sediments from one site in each lake. Site L1 was chosen arbitrarily, and site M1 was chosen because this site was suspected of being the most contaminated; the higher toxicity of site M2 sediments had not yet been determined. Mortality in 1 week was minor and matched survival in similar experiments with laboratory animals reasonable well (Table 4). Furthermore, zinc and copper accumulation by Loken Lake *Hyalella* was very similar to accumulation by laboratory-reared animals originating from southern Ontario (Table 5), suggesting that the source of animals and long-term laboratory culture do not affect zinc and copper accumulation. It should, therefore, be possible to extrapolate results obtained with laboratory animals to field conditions.

Not surprisingly, based on the toxicity of Manitouwadge sediments, amphipods could not be collected for metal analysis on sediments from this lake. A few amphipods were, however, collected from weeds along the shoreline near sites M2 and M3. These animals had much lower metal concentrations than did *Hyalella* exposed to M2 and M3 sediments in the laboratory (Table 5). Long-term regulation of body copper has been

Fig. 6. Final geometric mean wet mass of *Hyalella azteca* exposed to cotton gauze or sediments from Loken (L1, L2, L3) or Manitouwadge Lake (M1, M2, M3) for 4 weeks with either Lake Ontario tap (open bars) or site (solid bars) water. Gauze controls were exposed to Lake Ontario (left), Loken Lake (centre), and Manitouwadge Lake (right) water. Diamonds indicate results from experiments repeated after 1 year using stored sediments. Error bars are ± 1 SE.

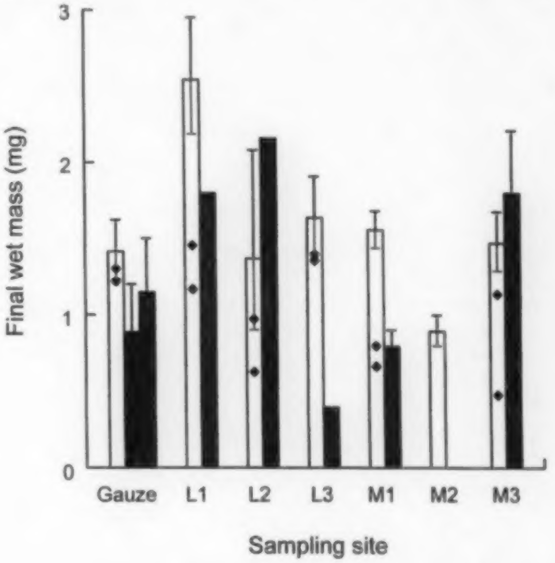


Table 4. Mean percent survival (with range given in parentheses) for laboratory ($n = 4$) and wild (Loken Lake, $n = 3$) *Hyalella* exposed to gauze or sediments from sites L1 and M2 for 1 week using either laboratory water (Lake Ontario) or water collected from Loken or Manitouwadge Lake.

	Laboratory animals			
Site	Ontario water	Loken water	Manitouwadge water	Loken animals in Loken water
Gauze	98 (90–100)	95 (95–95)	89 (80–100)	96 (95–100)
L1	90 (75–100)	61 (50–80)	—	77 (68–84)
M1	80 (75–85)	—	63 (40–80)	81 (79–84)

Table 5. Zinc and copper concentrations in laboratory cultured (n = 22–32) and Loken Lake (n = 18) *Hyalella* (± 95% confidence limits) exposed to gauze or sediments for 1 week, and in wild *Hyalella* (n = 10) collected from Loken and Manitouwadge lakes.

Site	Laboratory animals	Loken Lake animals	Wild animals
	Zinc (μmol/g dry mass)		
GL*	0.70 (0.61–0.84)	0.94 (0.86–1.08)	—
L1	0.83 (0.79–0.92)	0.85 (0.75–1.01)	0.81 (0.74–0.95)
M1	4.59 (4.25–5.25)	4.37 (3.69–5.49)	—
M2	8.36 (7.08–10.46)	—	1.82 (1.52–2.31)
M3	4.31 (3.72–5.28)	—	1.54 (1.36–1.84)
	Copper (μmol/g dry mass)		
GL*	1.49 (1.36–1.64)	1.46 (1.32–1.61)	—
L1	1.03 (0.90–1.18)	1.37 (1.29–1.45)	0.77 (0.69–0.86)
M1	2.85 (2.60–3.13)	2.20 (1.97–2.47)	—
M2	2.31 (2.06–2.58)	—	1.02 (0.76–1.36)
M3	3.00 (2.78–3.25)	—	0.89 (0.73–1.07)

Note: *GL, cotton gauze and Loken Lake water.

demonstrated in *Hyalella*, so the normal levels of copper are not surprising. Zinc, however, is not regulated in this fashion (Borgmann et al. 1993; Borgmann and Norwood 1995*a*). This means that either (*i*) animals have adapted genetically through selection over multiple generations or (*ii*) amphipods are surviving in microhabitats where metal contamination is not as severe as in the main portion of the lake (e.g., among vegetation where high organic matter complexes metals). This demonstrates that use of wild animals alone is not a satisfactory method of estimating metal availability and toxicity. Animals from the laboratory, or from uncontaminated sites, must be exposed to environmental samples under controlled conditions to clearly quantify metal availability and effects.

Discussion

The bioaccumulation of zinc from Manitouwadge Lake sediments by *Hyalella* demonstrates that toxicity of these sediments is almost certainly due to zinc. Furthermore, the similarity between uptake in 1- and 4-week exposures (Figs. 2A and 2B) is consistent with the rapid approach to equilibrium in waterborne exposures (Borgmann and Norwood 1995*a*), and demonstrates that exposures of only a 1-week duration can be used to infer chronic zinc toxicity. Although toxicity was slightly greater when site water rather than tap water (Lake Ontario) was used (Fig. 1), metal accumulation patterns were similar between site and tap water (Fig. 2), suggesting that tap water can, at least in some cases, be used in place of site water when collection of site water is impractical. The correlation between toxicity and zinc accumulation (Figs. 1, 2A, and 2B) is, by itself, suggestive of a cause and effect relationship, but it does not prove that zinc is the toxic agent because toxicity could be due to some other contaminant that happens to be present at concentrations correlating with those of zinc. It is the close similarity in the uptake–toxicity relationship to that obtained with zinc-spiked Hamilton Harbour sediments (Fig. 3) that provides the strongest case for attributing toxicity to zinc. In contrast, sediment zinc concentrations do not correlate with toxicity, because zinc bioavailability varies from site to site (Fig. 4). Similarly, zinc and copper in fish among lakes in this region correlate better with water concentrations than with sediment concentrations (Miller et al. 1992), also implying that metal bioavailability from sediments is not constant. The difficulty in predicting biological effects due to variations in metal bioavailability in sediments is well recognized (Luoma 1989; Ankley et al. 1994; Krantzberg 1994). Bioaccumulation, on the other hand, is a much better predictor of toxicity in sediments (Fig. 3). The correlation between toxicity and bioaccumulation of cadmium, but not between toxicity and water concentrations of cadmium, has also been demonstrated in *Hyalella* (Borgmann et al. 1991).

The relationship between toxicity and metal accumulation is not always constant and can be expected to vary depending on the form of metal exposure. The form of the toxicity–accumulation relationship, and the body concentration at which chronic toxicity occurs, varied between water and spiked sediment exposures (Borgmann and Norwood 1995*a*, 1997). The form of exposure could affect toxicity by changing the internal distribution of the metal. For example, mercury accumulates mainly in the gills of mayflies during waterborne exposures, but in the gut during sediment exposures (Saouter et al. 1993). Accumulation of zinc and cadmium from contaminated sediments also appears to be mainly in the gut (gut contents excluded) of mayflies (Hare et al. 1991). This may also be the case for *Hyalella* exposed to metal-contaminated sediments but is less likely to be the case during waterborne exposures. Cadmium accumulation at the 4- to 6-week LC50 was also slightly higher in cadmium-spiked sediments than in waterborne exposures (Borgmann et al. 1991).

Alternatively, the higher body concentration at the 4-week LC25 during spiked sediment exposures could be due to zinc in the gut contents (Borgmann and Norwood 1997). Unfortunately, the rapid excretion rate of body zinc (Borgmann and Norwood 1995*a*) precludes placing animals in uncontaminated water to allow time for gut clearance before zinc analysis. Nevertheless, total body zinc did correlate well with toxicity for sediments from two different sources (Fig. 3). The use of total body metal may be a useful indicator of effects in sediments even if some of the metal is present in the gut because this metal is associated with particles that have been selected for ingestion by *Hyalella*. If gut contents do account for much of the zinc accumulated from Manitouwadge sediments, then the lower accumulation of zinc from the more highly contaminated M1 sediments would imply that *Hyalella* is not selecting highly contaminated particles for ingestion, and this, in turn, affects toxicity. The net result is a total body zinc concentration indicative of zinc toxicity.

Copper accumulation was not sufficient to contribute to toxicity in 1-week tests (Fig. 5A). Although the toxicity–accumulation relationship cannot be used to unambiguously infer chronic toxicity, the absence of a clear growth reduction implies that the contribution of copper to chronic mortality is minimal (Borgmann and Norwood 1997). In contrast, the reduced growth in *Hyalella* exposed to copper-contaminated sediments from the Keweenaw Peninsula, Michigan (Kubitz et al. 1995), and reduced growth in sediments from the Clark Fork River, Montana (Ingersoll et al. 1994), implies that copper does contribute to toxicity at these sites.

The results of these laboratory exposures correlate well with observations in the field. *Hyalella* were absent from the surface of sediments collected in Manitouwadge Lake but abundant in Loken Lake. Survival and metal accumulation by Loken Lake *Hyalella* was similar to that of laboratory populations (Tables 4 and 5), suggesting that animals from southern Ontario are valid test organisms for extrapolation to field conditions further north. Metal concentrations in wild animals are not, however, indicators of potential toxicity, possibly owing to adaptation or microhabitat selection (Table 5). Animals must be exposed to environmental samples under controlled conditions in the laboratory. The impact of sediment toxicity on invertebrates, leading to reduced growth rate in fish in Manitouwadge Lake (Munkittrick and Dixon 1988; Munkittrick et al. 1991), also demonstrates that effects predicted from metal accumulation by *Hyalella* in the laboratory are not relevant just to benthic invertebrates but can be indicative of effects further up the food chain as well.

Zinc, and especially copper, are the metals for which prediction of effects from toxicity–accumulation relationships is most difficult. These metals are essential for life and are always present in high concentration (Borgmann and Norwood 1995*b*), making determination of small increases due to environmental contamination tedious. An increase of only two- to three-fold in body concentrations can result in substantial toxicity (Table 2). Nonregulated metals such as cadmium, lead, and mercury, on the other hand, are present at much lower concentrations in control animals than in animals exposed at the toxic threshold (Borgmann et al. 1993). Although the toxicity–accumulation relationship is a powerful tool for predicting zinc and copper toxicity in environmental samples, it should be an equally useful tool for nonregulated metals and much easier to apply.

Acknowledgements

We thank Kelly Munkittrick for advice in selecting sampling sites and help in collecting sediment, water, and *Hyalella* samples. Mike Ryan assisted with the bioassays.

References

Ankley, G.T., Thomas, N.A., Di Toro, D.M., Hansen, D.J., Mahony, J.D., Berry, W.J., Swartz, R.C., Hoke, R.A., Garrison, A.W., Allen, H.E., and Zarba, C.S. 1994. Assessing potential bioavailability of metals in sediments: a proposed approach. Environ. Manage. **18**: 331–337.

Borgmann, U. 1994. Chronic toxicity of ammonia to the amphipod *Hyalella azteca*: importance of ammonium ion and water hardness. Environ. Pollut. **86**: 329–335.

Borgmann, U. 1996. Systematic analysis of aqueous ion requirements of *Hyalella azteca*: a standard artificial medium including the essential bromide ion. Arch. Environ. Chem. Toxicol. **30**: 356–363.

Borgmann, U., and Norwood, W.P. 1995*a*. Kinetics of excess (above background) copper and zinc in *Hyalella azteca* and their relationship to chronic toxicity. Can. J. Fish. Aquat. Sci. **52**: 864–874.

Borgmann, U., and Norwood, W.P. 1995*b*. EDTA toxicity and background concentrations of copper and zinc in *Hyalella azteca*. Can. J. Fish. Aquat. Sci. **52**: 875–881.

Borgmann, U., and Norwood, W.P. 1997. Toxicity and accumulation of zinc and copper from metal-spiked sediments in *Hyalella azteca*. Can. J. Fish. Aquat. Sci. **54**: 1046–1054.

Borgmann, U., Norwood, W.P., and Babirad, I.M. 1991. Relationship between chronic toxicity and bioaccumulation of cadmium in *Hyalella azteca*. Can J. Fish. Aquat. Sci. **48**: 1055–1060.

Borgmann, U., Norwood, W.P., and Clarke, C. 1993. Accumulation, regulation and toxicity of copper, zinc, lead and mercury in *Hyalella azteca*. Hydrobiologia, **259**: 79–89.

Hare, L., Saouter, E., Campbell, P.G.C., Tessier, A., Ribeyre, F., and Boudou, A. 1991. Dynamics of cadmium, lead, and zinc exchange between nymphs of the burrowing mayfly *Hexagenia rigida* (Ephemeroptera) and the environment. Can. J. Fish. Aquat. Sci. **48**: 39–47.

Ingersoll, C.G., Brumbaugh, W.G., Dwyer, F.J., and Kemble, N.E. 1994. Bioaccumulation of metals by *Hyalella azteca* exposed to contaminated sediments from the upper Clark Fork River, Montana. Environ. Toxicol. Chem. **13**: 2013–2020.

Krantzberg, G. 1994. Spatial and temporal variability in metal bioavailability and toxicity of sediment from Hamilton Harbour, Lake Ontario. Environ. Toxicol. Chem. **13**: 1685–1698.

Kubitz, J.A., Lewek, E.C., Besser, J.M., Drake, J.B., III, and Giesy, J.P. 1995. Effects of copper-contaminated sediments on *Hyalella azteca*, *Daphnia magna*, and *Ceriodaphnia dubia*: survival, growth and enzyme inhibition. Arch. Environ. Contam. Toxicol. **29**: 97–103.

Luoma, S.N. 1989. Can we determine the biological availability of sediment-bound trace elements? Hydrobiologia, **176/177**: 379–396.

Miller, P.A., Munkittrick, K.R., and Dixon, D.G. 1992. Relationship between concentrations of copper and zinc in water, sediment, benthic invertebrates, and tissues of white sucker (*Catostomus commersoni*) at metal-contaminated sites. Can. J. Fish. Aquat. Sci. **49**: 978–984.

Munkittrick, K.R., and Dixon, D.G. 1988. Growth, fecundity, and energy stores of white sucker (*Catostomus commersoni*) from lakes containing elevated levels of copper and zinc. Can. J. Fish. Aquat. Sci. **45**: 1355–1365.

Munkittrick, K.R., Miller, P.A., Barton, D.R., and Dixon, D.G. 1991. Altered performance of white sucker populations in the Manitouwadge chain of lakes is associated with changes in benthic macroinvertebrate communities as a result of copper and zinc contamination. Ecotoxicol. Environ. Safety, **21**: 318–326.

Saouter, E., Hare, L., Campbell, P.G.C., Boudou, A., and Ribeyre, F. 1993. Mercury accumulation in the burrowing mayfly *Hexagenia rigida* (Ephemeroptera) exposed to CH_3HgCl or $HgCl_2$ in water and sediment. Water Res. **27**: 1041–1048.

Carotenoid pigment profiles distinguish anadromous and nonanadromous brown trout (*Salmo trutta*)

A.F. Youngson, A.I. Mitchell, P.T. Noack, and L.M. Laird

Abstract: Carotenoid pigment profiles were determined in muscle tissue extracts of anadromous and nonanadromous brown trout (*Salmo trutta*). In nonanadromous fish, zeaxanthin, lutein, astaxanthin, canthaxanthin, and two unidentified pigments were detected in some or all individuals. In anadromous fish, only astaxanthin and lutein were detected. On the basis of carotenoid pigment profiles, it was possible to distinguish the anadromous and nonanadromous individuals examined in this study with complete accuracy.

Résumé : Les profils des pigments caroténoïdes dans des extraits de tissu musculaire de truites brunes (*Salmo trutta*) anadromes et non anadromes ont été déterminés. Chez certains ou chez la totalité des individus non anadromes, on a détecté la présence de zéaxanthine, de lutéine, d'astaxanthine, de canthaxanthine et de deux pigments non identifiés. Chez les poissons anadromes, seules l'astaxanthine et la lutéine ont été décelées. Dans la présente étude, il était possible de distinguer avec une précision totale les sujets anadromes des sujets non anadromes à partir des profils des pigments caroténoïdes.
[Traduit par la Rédaction]

Introduction

Current methods for characterising the demography of spawning populations of salmonids in relation to migratory life history are compromised by the technical difficulties of achieving random sampling. Thus, fixed traps intercept only migratory individuals. Equivalent capture of the different migratory types by active means, such as netting or electrofishing, is made difficult by the differences in body size that often typify the types. Finally, in many cases, migratory fish are highly mobile near spawning time and are often present near their spawning areas only for a short time.

Carotenoid pigments are synthesised de novo by primary producers and passed up the food chain (Goodwin 1984). The pigments are assimilated by salmonids and impart a characteristic pink or red coloration to the body tissues. Carotenoids accumulated by females are translocated to their ova during sexual development and, later on, alevins and fry carry maternal pigment for a short period after hatch and emergence (Craik and Harvey 1986). On this basis, previous studies have discriminated the progeny of female Atlantic salmon (*Salmo salar*) that have escaped from fish farms from the progeny of others, according to the presence of synthetic carotenoids used as flesh colorants in aquaculture (Lura and Saegrov 1991; Webb et al. 1991).

The present study was undertaken to determine whether qualitative differences in naturally accumulated carotenoids might form the basis of a similar method for distinguishing anadromous and nonanadromous salmonids and their progeny. Salmonid eggs, alevins, and fry are relatively large and yield sufficient pigment to permit profiling of the carotenoid content of individuals. If migratory types can be classified according to their carotenoid profiles, genetic studies, for example, might be facilitated by being based on the sampling, classification, and analysis of progeny rather than parents. Carotenoid pigments were examined in fish muscle to determine whether distinct carotenoid profiles typify anadromous and nonanadromous types. The brown trout (*Salmo trutta*) was used as the model species.

Materials and methods

Wild, resident (nonanadromous) trout were obtained by netting, angling, or electrofishing from a diverse range of freshwater locations in Scotland: Lochan Loin ($n = 6$), Loch Clair ($n = 6$), and the River Sheildaig ($n = 4$) in Wester Ross; Loch Loch ($n = 6$) in Perthshire; unnamed northern tributaries of Loch Assynt ($n = 6$) in Sutherland; the Rivers Don and Dee ($n = 12$) in Aberdeenshire; and the Lumphanan Burn ($n = 6$), a tributary of the River Dee that is isolated from the main catchment by an impassable waterfall. With the exception of the Lumphanan Burn, all the sampling sites have open access to the sea. None of the samples was obtained in proximity to salmonid rearing sites, a potential source of anthropogenic carotenoid input to scavenging trout.

Anadromous individuals (sea-trout) were obtained from sea nets on the Aberdeenshire coast ($n = 10$) and from the River Don ($n = 2$). The latter, although captured in freshwater, were distinguished from freshwater residents according to their size at age (determined by scale reading) and their appearance. Fish were stored frozen at −50°C before samples of dorsal muscle were obtained by dissection.

All solvents for carotenoid pigment extraction were high-performance liquid chromatography (HPLC) grade. Approximately 100 mg of dorsal muscle was homogenised (Polytron homogeniser, Kinematica GmbH, Switzerland, fitted with a 7-mm probe) in 1 mL of acetone. The homogeniser probe was washed with 1 mL of acetone

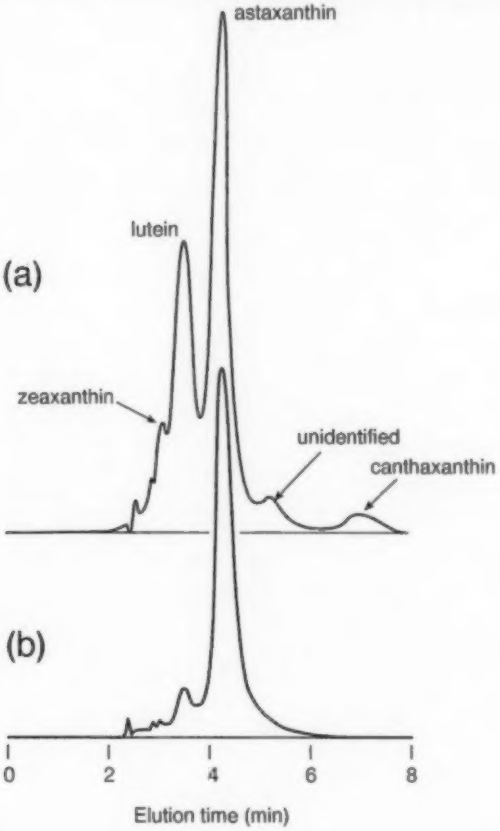
Received June 21, 1996. Accepted October 7, 1996.
J13514

A.F. Youngson[1] and A.I. Mitchell. SOAEFD Marine Laboratory, P.O. Box 101, Victoria Road, Aberdeen, AB11 9DB, U.K.
P.T. Noack and L.M. Laird. University of Aberdeen, Tillydrone Avenue, Aberdeen, AB24 3TZ, U.K.

[1] Author to whom all correspondence should be addressed. e-mail: youngsonaf@marlab.ac.uk

Can. J. Fish. Aquat. Sci. **54**: 1064–1066 (1997)

Fig. 1. HPLC chromatograms of carotenoid pigments in organic solvent extracts of muscle tissue from (*a*) nonanadromous trout showing five of the six components (the unidentified components eluting at 5.1 min is not present) detected in some or all cases and (*b*) anadromous trout showing the two peaks detected in all cases.



and this was combined with the extraction aliquot. *n*-Hexane (2 mL) was added to the acetone extraction volume and shaken. Distilled water (2 mL) was added to the organic solvent mixture, generating two phases. This mixture was centrifuged (MSE GF8 centrifuge) at 1000*g* for 10 min to aid separation of the aqueous and organic solvent phases. The organic solvent phase was removed and evaporated to dryness under a stream of nitrogen at room temperature. The resulting residue was redissolved in 0.5 mL of mobile-phase solvent (see below), passed through a 13-mm, 0.45-µm PTFE filter, and stored at −18°C in amber glass vials under nitrogen.

HPLC was carried out on a Waters modular system consisting of a 501 pump, U6K injector, 455 spectrophotometer, 740 data module, and 680 controller. A Hamilton PRP-1, 5-µm reverse-phase 250 × 4.1 mm column with a PRP-1 guard column was used. Elution was carried out isocratically using methanol–acetonitrile–dichloromethane, 40:48:12. This system yielded adequate separations of carotenoid pigments in a run time of 8 min. Detection was at 450 nm.

HPLC of tissue extracts commonly resolved six carotenoid components with retention times of 2.8, 3.2, 3.9, 4.4, 5.1, and 6.8 min. Zeaxanthin (2.8 min), astaxanthin (3.9 min), and canthaxanthin (6.8 min) were identified by reference to authentic standards (Hoffman-LaRoche, Basle, Switzerland). Lutein (3.2 min) was identified by its retention time relative to astaxanthin. Identity could not be established for peaks eluting at 4.4 and 5.1 min. The latter are therefore referred to throughout according to their retention times under the elution conditions used.

Table 1. Median proportional representation of six carotenoid pigments detected in a sample of 46 nonanadromous brown trout (range of values also indicated).

Pigment component	Median value (%)	Maximum value (%)	Minimum value (%)
Zeaxanthin	4.3	25	0
Lutein	25	60	0
Astaxanthin	61	90	30
4.4 min	Trace	Trace	0
5.1 min	2.0	10	0
Canthaxanthin	Trace	21	0

HPLC peaks for single, quantifiable pigment components were integrated by the 740 data module. Peak size was expressed as a percentage of the total integrated area. Components present in quantities that were not discriminated as separate peaks by the integrator were identified by inspection of chromatograms and denoted as trace.

Results

Among nonanadromous trout, six carotenoids were resolved in some or all of the 46 individuals examined (Fig. 1*a*). Astaxanthin was detected in all individuals: lutein was detected in all individuals, with a single exception. Zeaxanthin and the unidentified pigment eluting at 4.4 min were detected in 43% and 89% of the fish examined. In the latter case, levels did not exceed trace in any sample. The unidentified peak eluting at 5.1 min and canthaxanthin were detected in 93% and 74% of cases, respectively. Median values and ranges for the representation of all six carotenoid components are presented in Table 1.

The representation of carotenoid components in nonanadromous trout varied among sites. The representation of astaxanthin and lutein, for example, varied significantly among sampling locations (Kruskal–Wallis test; $P < 0.0001$ in both cases).

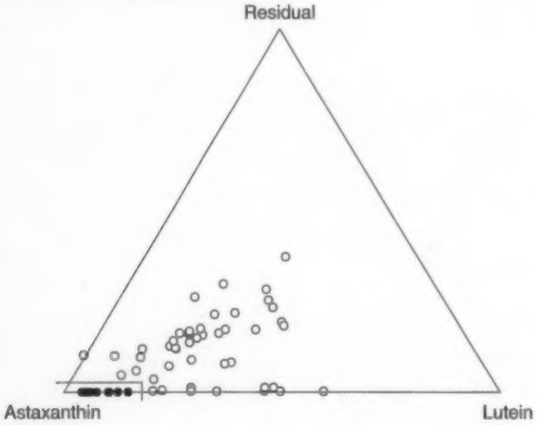
Both lutein and astaxanthin were resolved in extracts of tissues obtained from all anadromous trout sampled. No other components were detected (Fig. 1*b*). Lutein was represented with a median value of 6.8% (range 4.1–15%) of trace area, and astaxanthin was represented at a median value of 93% (range 85–96%).

The discriminatory power of carotenoid pigment profiles was examined using a triangular plot of the proportional representations of lutein, astaxanthin, and the residual part of the peak area attributable to the other carotenoid components. Total separation of the anadromous and nonanadromous groups examined was achieved (Fig. 2).

Discussion

As expected (e.g., see Craik and Harvey 1987), astaxanthin was the dominant pigment in extracts of tissue prepared from anadromous trout. Lutein was the only other component detected. Astaxanthin and lutein were also major components of the pigment profile in nonanadromous trout, but relative to anadromous fish, astaxanthin was less and lutein more strongly represented. This difference alone was highly discriminatory for the migratory classes.

Fig. 2. Triangular plot of the proportional representations of astaxanthin, lutein, and the residual part of the total chromatogram area. Data for 12 anadromous (solid circles) and 46 nonanadromous (open circles) fish are shown.



Complete discrimination was achieved by considering an additional, mixed group of pigments (zeaxanthin, canthaxanthin, and the unidentified pigments eluting at 4.4 and 5.1 min) that were variably represented in the tissue pigment profiles of many of the nonanadromous trout. In view of the strong link between the pigment load of females and their progeny, a similar level of discrimination of maternal pigment burdens in the eggs and alevins of anadromous and nonanadromous females is likely to be possible.

Further, pigment profiles varied significantly among groups of nonanadromous trout sampled from different locations, presumably because of corresponding differences in the representation of the carotenoids in their diet. This indicates that carotenoid pigment profiling may find an application as a discriminator among groups of nonanadromous fish exploiting different feeding locations, or different feeding niches in the same freshwater locations. However, further study will be necessary to test the power of this approach.

Acknowledgements

This study was performed collaboratively under the auspices of the Aberdeen Research Consortium. The study was supported by the Ministry for Agriculture, Fisheries and Food (Project No. SF 0104) and by the Scottish Office Agriculture, Environment and Fisheries Department.

References

Craik, J.C.A., and Harvey, S.M. 1986. The carotenoids of eggs of wild and farmed salmon and their changes during development. J. Fish Biol. **29**: 549–565.

Craik, J.C.A., and Harvey, S.M. 1987. A biochemical method for distinguishing between wild and farmed salmonid fishes by their carotenoid pigmentation. J. For. Sci. Soc. **27**: 47–55.

Goodwin, T.W. 1984. The biochemistry of the carotenoids. Vol. 2. Animals. Chapman and Hall, London.

Lura, H., and Saegrov, H. 1991. A method of separating offspring from farmed and wild Atlantic salmon (*Salmo salar*) based on different ratios of optical isomers of astaxanthin. Can. J. Fish. Aquat. Sci. **48**: 429–433.

Webb, J.H., Cunningham, P.D., Hay, D.W., and Youngson, A.F. 1991. The spawning behaviour of escaped farmed salmon and wild salmon (*Salmo salar* L.) in a northern Scottish river. Aquaculture, **98**: 97–110.

Larval parameters determining preschooling juvenile production of Pacific saury (*Cololabis saira*) in the northwestern Pacific

Yoshiro Watanabe, Yoshioki Oozeki, and Daiji Kitagawa

Abstract: Production of larvae in the hatching size-class of Pacific saury (*Cololabis saira*) was highest in autumn 1990–1994, implying that spawning activity was highest in this season. Growth and mortality rates were stable in the winter-spawned cohorts in Kuroshio waters (south of Honshu); variable rates were found in the autumn- and spring-spawned cohorts in the mixed water region to the northeast. Although no particular period of high mortality was detected through the larval and juvenile stages, overall percent survival through the larval and juvenile stages differed by an order of magnitude among seasons. Production of 40-mm preschooling juveniles was determined by larval production in the smallest size-class in the winter cohort, but by overall percent survival through the larval and juvenile stages in the spring and autumn cohorts. Over the last 44 yr, percentage of winter-spawned cohorts in commercial catches was stable, compared with large interannual variations of autumn- and spring-spawned cohorts. These observations were assumed to stem from stable juvenile production in winter and variable production in autumn and spring, suggesting the possibility of recruitment forecasts of seasonally spawned cohorts of saury based on preschooling juvenile production estimates in the northwestern Pacific.

Résumé : La production de larves de la classe de taille « éclosion » du balaou japonais (*Cololabis saira*) était la plus élevée en automne 1990–1994, ce qui suppose que l'activité de frai était la plus forte au cours de cette saison. Les taux de croissance et de mortalité étaient stables dans la cohorte ayant frayé l'hiver dans les eaux du Kuroshio au sud de Honshu; des taux variables ont été observés dans les cohortes de frai d'automne et de printemps dans la région des eaux mélangées au nord-est. Bien qu'aucune période particulière de mortalité élevée n'ait été décelée au cours des stades larvaires et juvéniles, le taux de survie global jusqu'à ces stades a varié par un ordre de grandeur entre les saisons. La production de juvéniles de 40 mm avant rassemblement en bancs a été déterminée par la production de larves dans la plus petite classe de taille dans la cohorte d'hiver et par le taux de survie global jusqu'aux stades larvaires et juvéniles dans les cohortes de printemps et d'automne. Au cours des 44 dernières années, le pourcentage des cohortes d'hiver dans les prises commerciales a été stable, comparativement à de grandes variations interannuelles dans le cas des cohortes de printemps et d'automne. On a supposé que ces observations proviennent d'une production stable de juvéniles en hiver et d'une production variable au printemps et en automne, ce qui laisse supposer la possibilité de pouvoir prévoir le recrutement des cohortes de balaou à frai saisonnier à partir des valeurs estimées de la production de juvéniles avant rassemblement en bancs dans le nord-ouest du Pacifique.

[Traduit par la Rédaction]

Introduction

Pacific saury (*Cololabis saira*) is a major pelagic commercial fish in the northwestern Pacific. The total catch of saury has fluctuated greatly over the last 44 yr, ranging from 575 000 tonnes (t) in 1958 to 52 000 t in 1969. Coefficient of variation (CV) in the catches was 45.1% in the 44 yr after 1951 (Japan Saury Fishery Association 1995). Large fluctuations in the catch of saury were observed not only in weight of landings but also in size composition. Percent catch in number of sauries in size categories varied year by year (Table 1). The large-size sauries, which constitute 31.1% in number and more than 50% in weight of catches, fluctuated from 0.7 to 75.9% in number of the total catch, and its CV was as large as 63.8%.

The saury achieves 30 cm adult size in about 1 yr (Watanabe et al. 1988), and therefore the recruiting year-class is considered to constitute a major part of the population (Fukushima et al. 1990). Matsumiya and Tanaka (1978) demonstrated that the population of the saury is seriously affected by reproductive success or failure. The large interannual fluctuations in weight of landings and size composition are thought to result from interannual variability in population reproduction. Spawning of the saury starts in September and continues until June, shifting location from spawning grounds in the mixed-water region and the Kuroshio waters in the northwestern Pacific (Fig. 1) (Odate 1977; Watanabe and Lo 1989). The saury population in the northwestern Pacific is composed of autumn-, winter-, and spring-spawned cohorts. The three cohorts seem to correspond to the large, medium, and small size categories of landed sauries. The autumn-spawned cohort corresponds to the large size of 1-yr-olds, the winter-spawned to the medium size of 8- to 10-mo-olds, and the spring-spawned cohort to the small size of <6-mo-olds (Fukushima et al. 1990). As the proportions of the young and extra-large categories

Received March 19, 1996. Accepted October 7, 1996.
J13359

Y. Watanabe.[1] Ocean Research Institute, University of Tokyo, 1–15–1 Minamidai, Nakano-ku, Tokyo 164, Japan.
Y. Oozeki. National Research Institute of Fisheries Science, 2–12–4 Fukuura, Kanazawa-ku, Yokohama 236, Japan.
D. Kitagawa. Hachinohe Branch, Tohoku National Fisheries Research Institute, 25–259 Shimo-mekurakubo, Same, Hachinohe 031, Japan.

---

[1] Author to whom all correspondence should be addressed. e-mail: ywatanab@ori.u-tokyo.ac.jp

Table 1. Range, mean, and SD in percentage of landed sauries in the five size categories over 44 yr, 1951–1994.

Fish size		Size composition (%)			
Category	Range (mm)	Range	Mean	SD	CV (%)
Young	<200	0–37.8	2.6	6.1	236.7
Small	200–239	0.2–39.8	12.0	11.7	97.0
Medium	240–289	15.1–79.8	51.0	17.1	33.5
Large	290–319	0.7–75.9	31.1	19.9	63.8
Extra large	>320	0.1–21.8	3.3	4.2	126.1

were usually small (Table 1), relative levels of reproduction in the three spawning seasons reflect the size composition of the saury population, and the sum of them constitutes the total population of the saury.

The Pacific saury lays adhesive eggs with filaments that attach to floating objects such as drifting sea algae, so it is difficult to estimate egg abundance quantitatively. However, larval production can be estimated from plankton sampling. Mortality curves for saury can be constructed from data on abundance of fish in various size-classes (Watanabe and Lo 1989). Daily growth rates may be estimated from otolith readings (Watanabe et al. 1988). In this paper, we analyze production of larvae in the hatching size-class and growth and mortality in the larval and juvenile stages over the three spawning seasons for five years (1990–1994), and estimate the daily production of preschooling juveniles in each season. Annual variability of juvenile production is interpreted in terms of three parameters (larval production, growth, and mortality) and the environmental factors determining growth and mortality in each season.

Data sources and methods

Field collections

Spawning grounds of the Pacific saury shift seasonally depending on sea surface temperatures. Spawning occurs in the mixed-water region between the Oyashio front and the Kuroshio Extension in the early-spawning season (autumn), in and around the Kuroshio waters in the midspawning season (winter), and in the mixed-water region again in the late-spawning season (spring) (Fig. 1). Larval and juvenile censuses were conducted during the three spawning seasons of the five years from 1990 to 1994 by research vessels from three National Fisheries Research Institutes and seven fisheries experimental stations of local governments. Some of the research cruises were dedicated to saury larval and juvenile censuses, and others were for egg and larval surveys of other small pelagic fish species and adult skipjack tuna (*Katsuwonus pelamis*). We used data from sampling stations with at least one saury larva or juvenile.

Saury larvae <25.0 mm knob length (KnL: distance from the tip of lower jaw to the posterior end of muscular knob on the caudal peduncle (Kimura 1956)) and juveniles ≥25.0 mm KnL were collected in the autumn (September–December), winter (January–March), and spring (April–June) spawning seasons using a cylindrical–conical net with 1.3-m-diameter mouth and 0.45-mm-mesh aperture. The length of the side of the cylinder section was 2.5 m and that of the conical section was 3.0 m. As saury larvae and juveniles are distributed in the epipelagic stratum (Odate and Hayashi 1977), the net is towed on the sea surface for 10 min at 2 kn ($1.03\ \mathrm{m \cdot s^{-1}}$). Sea surface area covered by a tow is 803 $\mathrm{m^2}$ ($1.03\ \mathrm{m \cdot s^{-1}} \times 600\ \mathrm{s} \times 1.3\ \mathrm{m}$). The net was not equipped with a flowmeter and fish abundance was expressed in number per unit sea surface area (square kilometres). In spite of possible net evasion by larval and juvenile sauries (Smith and Richardson 1977), we towed the net by three bridles in front of the mouth opening because of its easy operation. With this method, we covered extensive spawning areas in the three seasons by conducting a large number of net tows. Net tow samples were preserved in 5% seawater–formalin for KnL measurements or in 80% ethanol for both KnL measurements and otolith readings. For each of the 14 spawning seasons, a total of 58–391 tow samples were collected, 906–9500 saury larvae and juveniles were sorted out from the samples and KnL measured to the nearest 0.1 mm for constructing a frequency distribution in size-classes, and 40–339 pairs of sagittal otoliths were dissected out of fish for establishing a growth curve over each season (Table 2).

Corrections for body shrinkage and catch efficiency

KnL measurements were corrected for shrinkage due to 5% formalin preservation by multiplying by a factor of 1.12 for fish <9.9 mm and 1.01 for those >10.0 mm (Oozeki et al. 1991). For specimens preserved in 80% ethanol, we used a correction factor of 1.08 for fish <9.9 mm and 0.98 for those >10.0 mm (Oozeki et al. 1991). Larvae and juveniles in each tow sample were classified into eight size-classes of 5-mm intervals: <9.9, 10.0–14.9,..., 40.0–44.9 mm corrected KnL. Sauries begin to school at about 50 mm KnL (Watanabe and Kuji 1991). Juveniles >45.0 mm were not included in the size frequency analyses due to low catchability. Numbers of fish per net tow in the size-classes were corrected for diel differences in catch efficiency of the net using time-of-day and size-dependent correction factors (Watanabe 1990). After the corrections, we obtained the KnL frequency distribution of each tow sample. Mean number of fish per square kilometre of sea surface area in the eight size-classes in each spawning season was calculated from all net tow samples.

Growth curve

Parallel with the above procedures, otoliths were removed from fish and examined to establish growth curves for the seasonally spawned cohorts. Since no particular inshore–offshore trend in growth rate was detected in preliminary observations, two to five ichthyoplankton samples were selected from different temperature zones in each season and 30–50 fish specimens were processed for otolith examination from each sample. Fish from all size-classes including those >45.0 mm were selected from ethanol-preserved samples to cover as wide a size range as possible. Sagittal otoliths were dissected from each specimen after measuring KnL, cleaned, and mounted with a clear enamel resin on a glass plate. The number of daily rings was counted using an otolith reading system consisting of a light microscope, a video camera and monitor, and an image analysis system. Otoliths were read by one reader and the counts were examined by one of the authors of this paper using video-image printouts of the measured otoliths in order to minimize counting errors. As saury larvae have five rings in their otoliths when hatched (Watanabe and Kuji 1991), daily age of fish was calculated to be the total number of rings minus 5. We pooled all the otolith data for a spawning season and plotted the size-at-age distribution.

An exponential, the Gompertz, and logistic growth models were applied to length-at-age data. For fittings of the Gompertz and logistic models, we used the computation programs of Akamine (1986). The Gompertz model fitted best to the data sets from the 14 spawning seasons and we used the model to describe the growth curve of young saury. The model is expressed as

$$L_t = L_\infty \cdot \exp(-\exp(-K(t - t_f)))$$

where L_t and L_∞ are KnL (millimetres) at age t and infinity, K is a nondimensional growth coefficient, and t_f is an age at the inflection point of the Gompertz growth curve. Watanabe et al. (1988) estimated KnL at hatching after net abrasion and before preservation to be 5.9 mm and fixed the 0-intercept at 5.85–5.95 mm in their computation of the growth curve. As we had many otolith data points in the hatching size-class, we did not fix the 0-intercept in the growth model fitting in this study.

Fig. 1. Schematic illustration of spawning ground distribution of the saury in autumn, winter, and spring in relation to oceanographic structures.

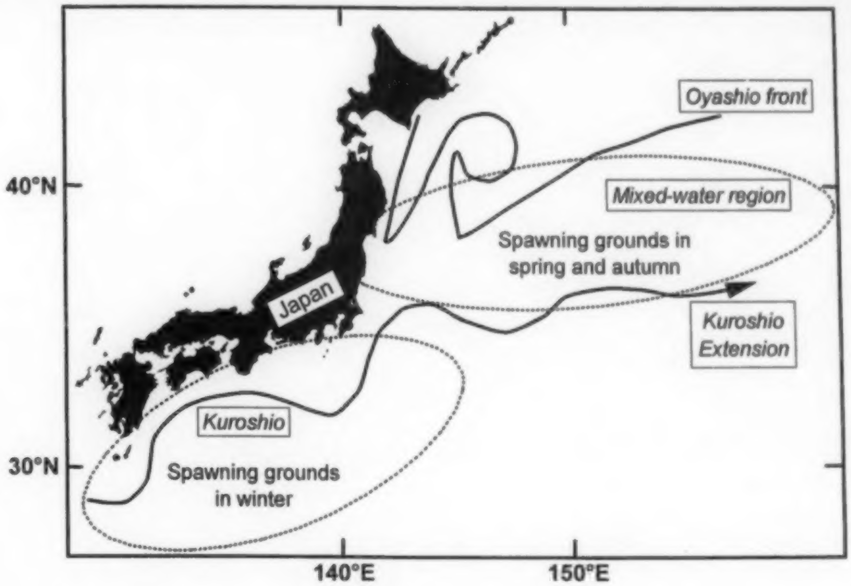


Table 2. Number of samples used for establishing growth and mortality curves for three spawning seasons over five years.

			Total number of fish for:	
Year	Spawning season	Total number of net tow samples	size measurement	otolith reading
1990	Winter	58	906	40
	Spring	239	2723	89
	Autumn	78	2199	267
1991	Winter	219	1405	186
	Spring	383	2461	115
	Autumn	180	9500	339
1992	Winter	324	4493	339
	Spring	231	3711	195
	Autumn	387	6966	244
1993	Winter	89	996	220
	Spring	330	6126	181
	Autumn	361	8725	196
1994	Winter	170	4742	250
	Spring	391	6959	104
	Autumn	—	—	—

The amount of size-at-age data was larger in the larval stage than in the juvenile stage, and this nonuniform data distribution over the age range may cause a biased growth curve. We examined the distributions of residuals of the growth curve fittings and found them even over the age range up to about 60 d.

Mortality curve

Based on the growth rates for each season, we calculated midages and durations in days of the eight size-classes at 5-mm intervals. The size range of the smallest size-class was fixed at 5.9–9.9 mm and a midsize at 7.9 mm. The mean number of fish (per square kilometre) in each of the eight size-classes was divided by duration of the corresponding size-classes, and daily fish production was obtained for each size-class. Estimates of daily production of each of the eight size-classes were then plotted against the midages of the size-classes and the plots were fitted to an exponential decay model (Watanabe and Lo 1989):

$$P_t = P_0 \cdot \exp(-Z \cdot t)$$

where P_t is daily fish production (per square kilometre) at age t, P_0 is daily larval production (per square kilometre) at age 0, and Z is daily instantaneous mortality rate.

Age of preschooling juveniles at 40 mm KnL (t_{40}) for each season was calculated by the growth formula. Daily production of 40-mm juveniles (per square kilometre), $P_{t_{40}}$, was calculated as

$$P_{t_{40}} = P_0 \cdot \exp(-Z \cdot t_{40})$$

and used as an index of population reproduction.

Results

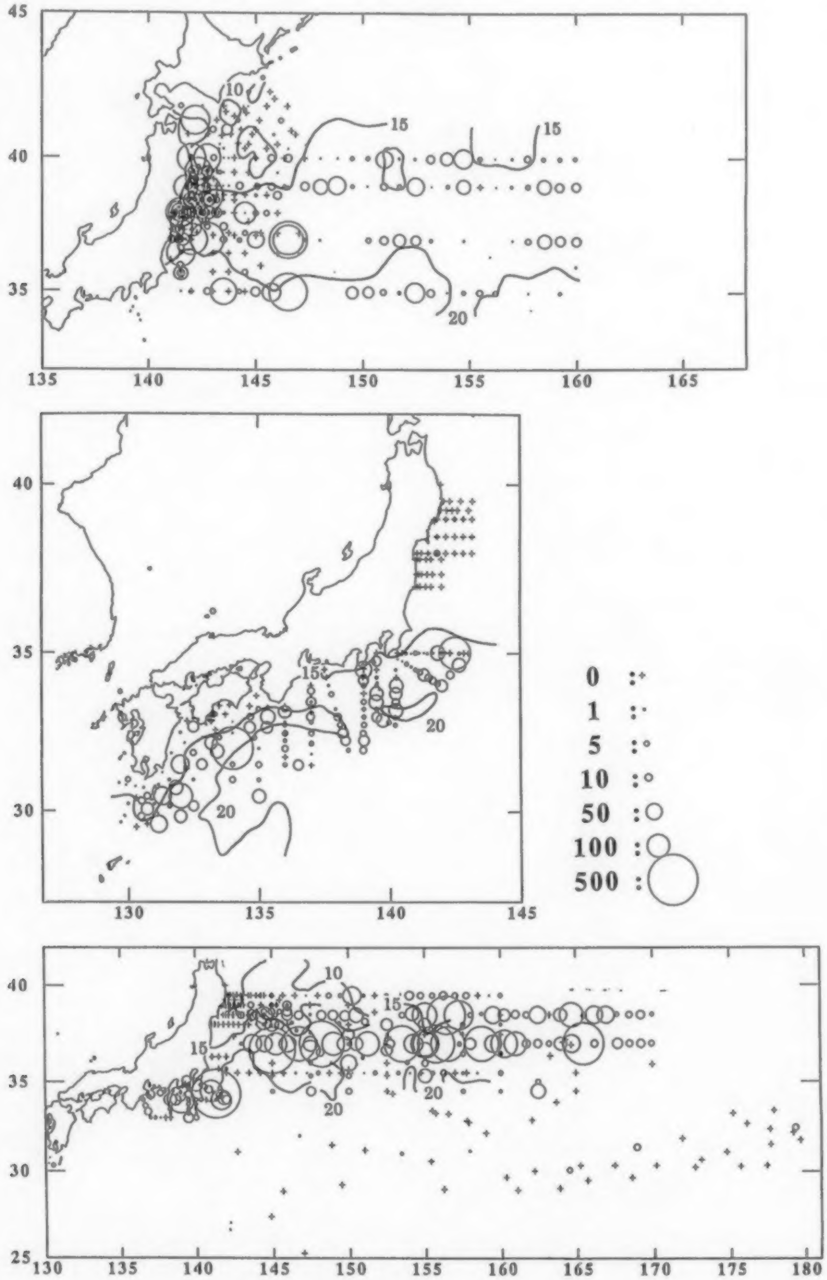
Distribution of larvae

Distribution of saury larvae in the autumn spawning season extends from the coastal waters of northern Japan to offshore waters further than 160°E between the Oyashio front and the Kuroshio Extension in the northwestern Pacific (Fig. 2). Sea surface temperatures at net tow stations containing larvae ranged from 13 to 22°C. Most of the larvae were distributed between 15 and 21°C.

In winter, the distribution range extended to more southerly waters along and offshore of the Kuroshio Current south of western and eastern Japan. Few larvae were collected in coastal waters off northern Japan. The sea surface temperature at net tow stations positive for saury collection in winter ranged from 16 to 22°C. The majority of the larvae was distributed along the isotherm at 20°C.

Saury larvae were distributed in the mixed-water region in spring, extending from coastal areas to as far offshore as 170°E. Concentrated larval distribution was detected in the

Fig. 2. Distribution of saury larvae in autumn 1993 in the mixed-water region between the Oyashio front and the Kuroshio Extension (top panel), in winter 1994 in and offshore of the Kuroshio (middle panel), and in spring 1994 in the mixed-water region (bottom panel). Circles represent number of larvae per net tow ($803 \cdot m^{-2}$). Solid lines are isotherms of 10, 15, and 20°C drawn using the data from the saury census and other research cruises.

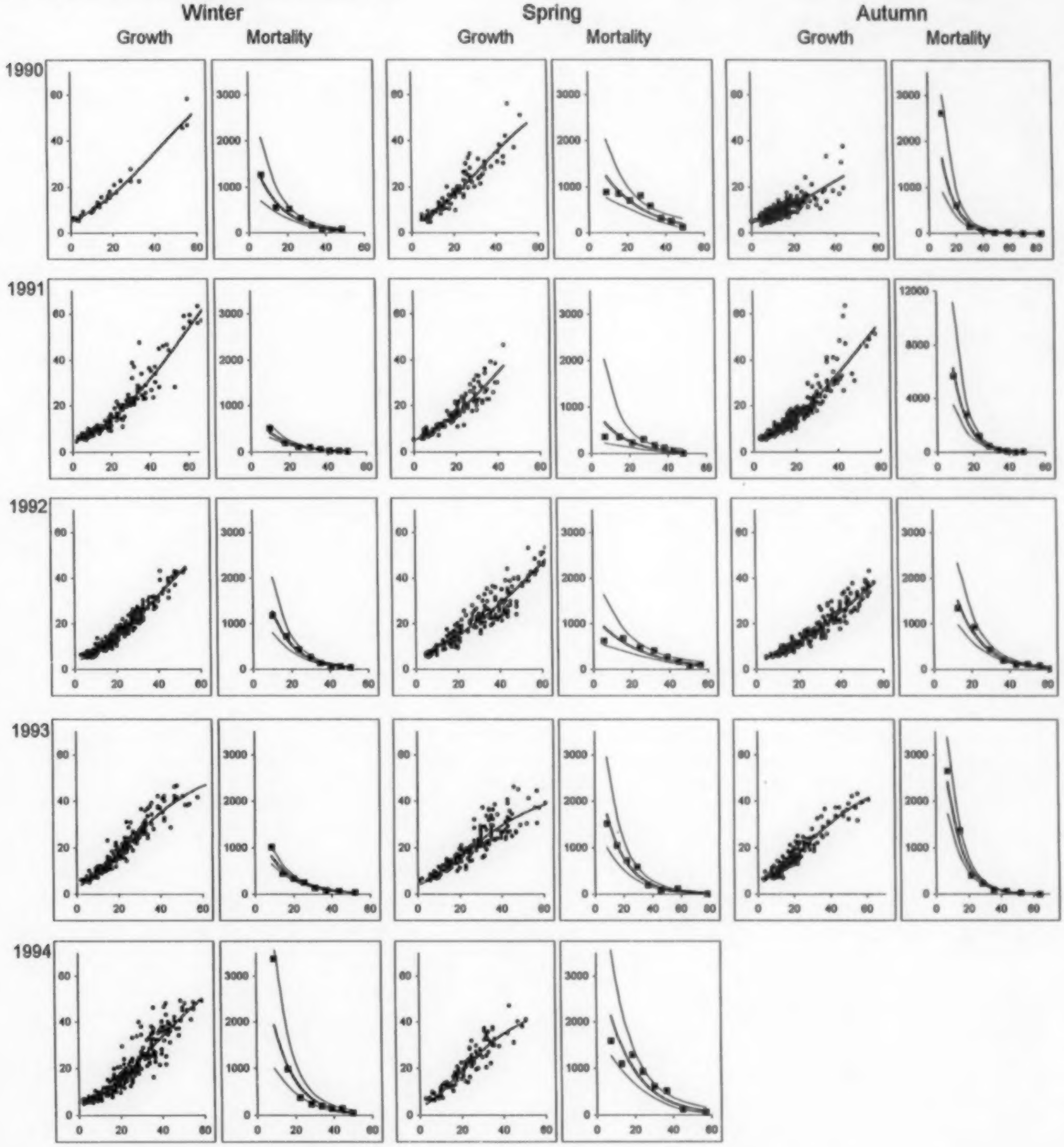

45
40
35
10
15
15
20
135
140
145
150
155
160
165
40
35
30
15
20
20
130
135
140
145
0 :+
1 :·
5 :∘
10 :○
50 :○
100 :○
500 :○
40
35
30
25
10
15
15
20
20
130
135
140
145
150
155
160
165
170
175
180

coastal waters off eastern Japan. Sea surface temperature in spring was in the range of 12–22°C. A large number of larvae were distributed between the isotherms of 15 and 20°C, but substantial distribution was detected in the waters north of the isotherm of 15°C.

Growth

Growth curves of saury showed interannual differences over the three seasons of the five years studied (Fig. 3). Infinite KnLs were large in winter 1991 (148.7 mm) and small in spring 1993 (46.5 mm) (Table 3). Maximum growth rates at

Fig. 3. Gompertz growth curves and exponential mortality curves for three spawning seasons over five years. Thin lines in the mortality panels indicate 95% confidence limits of the curve. The x-axis of each panel is age (d), and the y-axis of each growth panel is KnL (mm) and of each mortality panel is daily fish production ($\mathrm{km}^{-2}\cdot\mathrm{d}^{-1}$).



the inflection points of the Gompertz curves were highest in winter 1991, 1.15 $\mathrm{mm}\cdot\mathrm{d}^{-1}$ at the age of 60.7 d after hatching when juveniles were 54.7 mm KnL. Growth rate was lowest in spring 1993, 0.73 $\mathrm{mm}\cdot\mathrm{d}^{-1}$ at the age of 21.5 d when larvae were 17.1 mm KnL. Ages of juveniles 40 mm KnL varied from 45.3 (spring 1991) to 76.2 d (autumn 1990).

The Gompertz model fittings by Akamine's (1986) program are executed by iterations changing all three parameters (L, K, t_f), and therefore, they correlate each other. It is not valid to make between-season comparisons of fish growth in terms of single parameters. Rather than using the Gompertz parameters, we used the age of 40-mm juveniles (t_{40}) calculated from

Table 3. Parameters of Gompertz growth curves (L_{inf}, infinite KnL; K, growth coefficient; t_f, age at the inflection point), KnL (L_f) and daily growth rate (G_f) at the inflection points, age of 40-mm juveniles (t_{40}), and variance (Var) of the growth curve fitting (N is the number of fish used for the fittings).

Year	Season	N	L_{inf} (mm)	K	t_f (d)	L_f (mm)	G_f (mm·d^{-1})	t_{40} (d)	Var
1990	Winter	40	103.3	0.0252	43.6	38.0	0.956	45.6	4.7
	Spring	89	73.6	0.0352	31.6	27.1	0.954	45.7	14.6
	Autumn	267	57.9	0.0255	37.1	21.3	0.543	76.2	6.1
1991	Winter	186	148.7	0.0210	60.7	54.7	1.146	47.8	13.1
	Spring	115	115.4	0.0241	47.7	42.5	1.022	45.3	11.9
	Autumn	339	132.5	0.0234	53.1	48.7	1.141	45.4	10.7
1992	Winter	339	93.4	0.0283	41.9	34.4	0.973	47.8	3.8
	Spring	195	157.1	0.0164	72.2	57.8	0.945	53.1	16.5
	Autumn	244	94.7	0.0230	52.2	34.8	0.800	58.7	6.6
1993	Winter	220	56.3	0.0448	23.4	20.7	0.928	47.3	8.2
	Spring	181	46.5	0.0427	21.5	17.1	0.730	65.8	16.8
	Autumn	196	53.2	0.0380	24.4	19.6	0.743	57.3	5.9
1994	Winter	250	81.9	0.0313	36.2	30.1	0.942	46.8	17.9
	Spring	104	49.1	0.0511	19.1	18.1	0.923	50.1	13.0
	Autumn	—	—	—	—	—	—	—	—
Mean	Winter		96.7	0.0301	41.2	35.6	0.989	47.1	
	Spring		88.3	0.0339	38.4	32.5	0.915	52.0	
	Autumn		84.6	0.0275	41.7	31.1	0.807	59.4	
SD	Winter		33.9	0.0091	13.5	12.5	0.089	0.9	
	Spring		47.3	0.0139	22.0	17.4	0.110	8.4	
	Autumn		37.0	0.0071	13.7	13.6	0.249	12.7	
CV (%)	Winter		35.1	30.1	32.8	35.1	9.0	1.9	
	Spring		53.6	41.1	57.2	53.6	12.0	16.1	
	Autumn		43.7	25.8	32.8	43.6	30.8	21.3	

the growth curves as an index of growth in early life stages. The mean age of 40-mm juveniles (t_{40}) in winter was 47.1 ± 0.9 (SD) d after hatching, which is younger than in spring (52.0 ± 8.4) or in autumn (59.4 ± 12.7) (Table 3). The coefficient of interannual variations in t_{40} was small in winter (1.9%) in contrast with large variances in spring (16.1%) and autumn (21.3%).

Mortality and production

Daily larval production at the midage of the smallest size-class ($P_{t_{7.9}}$) in the spawning seasons ranged from 434 to 2417·km^{-2}·d^{-1} in the five years studied, with an exceptionally high value (6287·km^{-2}·d^{-1}) in autumn 1991 (Table 4). Daily mortality coefficients (Z) varied from 0.0439 to 0.1313, which corresponds to 4.3–12.3%·d^{-1}. Daily production of 40-mm preschooling juveniles ($P_{t_{40}}$) varied greatly among seasons over the five years, from 3.6 to 256.3·km^{-2}·d^{-1}.

Daily larval production ($P_{t_{7.9}}$) was highest in autumn (2964 ± 2251·km^{-2}·d^{-1}, mean ± SD). Daily mortality coefficients were large (0.1041 ± 0.0228) in this season and were effective over the seasonal minimum in growth rates (t_{40} = 59.4 ± 12.7) and hence resulted in the lowest daily production of preschooling juveniles, 38.5 ± 31.5·km^{-2}·d^{-1}. Daily larval production in winter and spring was at almost the same level, 1136 and 1344·km^{-2}·d^{-1}, respectively. Daily mortality coefficients in spring (0.0586 ± 0.0124) were smaller than in winter (0.0793 ± 0.0073) and resulted in higher production of preschooling juveniles in this season. Variances in daily rates of larval production, percent mortality, and preschooling juvenile production were large in the spring and autumn spawning seasons in the mixed-water region. CV's in daily percent mortality and preschooling juvenile production in winter were smallest, 8.8 and 36.7%, respectively, among the three seasons (Table 4).

Overall percent survival between the smallest size-class ($t_{7.9}$) and 40-mm juveniles (t_{40}) was calculated as $P_{t_{40}}/P_{t_{7.9}}$ (= $\exp(-Z(t_{40} - t_{7.9}))$) which was an integrated rate of growth and mortality through the larval and early juvenile stages. It varied in orders of magnitude from 0.11% in autumn 1990 to 19.7% in spring 1990. Among the three seasons, overall percent survival was high in spring and low in autumn. The CV in overall percent survival was small in winter (21.3%) compared with large variances in autumn and spring, 118.8 and 77.4%, respectively (Table 4).

Parameters determining juvenile production

Coefficients of determination of juvenile production ($P_{t_{40}}$) by larval production ($P_{t_{7.9}}$) and overall percent survival were calculated for each season. In winter, interannual variations in juvenile production could be explained at 86.8% ($P < 0.05$) by larval production, but only at 20.2% by percent survival (Fig. 4). On the other hand, variations in juvenile production in spring and autumn were explained by percent survival at 60.7 and 80.8%, respectively. Larval production explained only

Table 4. Production and mortality estimates of larval and juvenile sauries.

		Larval production			Mortality				Juvenile production			Survival (%)
Year	Season	$\ln(P_{t_{7.9}})$	SEM	$P_{t_{7.9}}$	Z	SEM	%·d^{-1}	R^2	$\ln(P_{t_{40}})$	SEM	$P_{t_{40}}$	$(P_{t_{40}}/P_{t_{7.9}})$
1990	Winter	7.10	0.220	1208.7	0.0731	0.0084	7.05	0.927	4.40	0.166	81.5	5.57
	Spring	7.13	0.200	1243.7	0.0466	0.0084	4.55	0.839	5.55	0.156	256.3	19.65
	Autumn	7.40	0.249	1638.4	0.1030	0.0059	9.79	0.981	1.27	0.202	3.6	0.11
1991	Winter	6.07	0.128	433.6	0.0750	0.0050	7.23	0.975	3.37	0.094	29.2	5.67
	Spring	6.51	0.454	669.8	0.0707	0.0177	6.83	0.728	3.96	0.339	52.4	4.95
	Autumn	8.75	0.236	6286.7	0.1313	0.0096	12.30	0.969	4.25	0.175	70.2	0.83
1992	Winter	7.15	0.187	1275.6	0.0870	0.0075	8.33	0.958	4.10	0.142	60.3	3.77
	Spring	6.85	0.228	940.5	0.0439	0.0071	4.30	0.865	4.88	0.167	131.3	12.34
	Autumn	7.32	0.176	1513.6	0.0755	0.0058	7.27	0.966	4.09	0.134	59.5	3.10
1993	Winter	6.71	0.094	823.8	0.0738	0.0038	7.11	0.984	4.13	0.077	61.9	5.65
	Spring	7.45	0.220	1722.5	0.0672	0.0062	6.50	0.951	4.14	0.186	62.7	2.08
	Autumn	7.79	0.138	2416.9	0.1066	0.0044	10.11	0.990	3.03	0.114	20.8	0.48
1994	Winter	7.57	0.270	1937.3	0.0874	0.0109	8.37	0.915	4.51	0.208	91.0	3.69
	Spring	7.67	0.213	2144.8	0.0648	0.0080	6.27	0.916	5.25	0.179	190.2	6.27
	Autumn	—	—	—	—	—	—	—	—	—	—	—
Mean	Winter			1135.8	0.0793		7.62				64.77	4.87
	Spring			1344.3	0.0586		5.69				138.60	9.06
	Autumn			2963.9	0.1041		9.87				38.52	1.13
SD	Winter			560.7	0.0073		0.67				23.79	1.04
	Spring			594.1	0.0124		1.18				86.27	7.01
	Autumn			2250.9	0.0228		2.06				31.52	1.34
CV (%)	Winter			49.37	9.19		8.82				36.73	21.33
	Spring			44.19	21.21		20.66				62.24	77.35
	Autumn			75.95	21.94		20.88				81.84	118.81

Note: $P_{t_{7.9}}$ is production of larvae in the hatching size-class (5.5–9.9 mm), Z is the daily instantaneous mortality coefficient, $P_{t_{40}}$ is daily production of 40-mm preschooling juveniles, and R^2 is the coefficient of determination of mortality curves. Overall percent survival was calculated as a proportion of juvenile production to larval production, $P_{t_{40}}/P_{t_{7.9}}$.

16.9 and 25.3% of juvenile production in spring and autumn, respectively. We examined a correlation between larval production ($P_{t_{7.9}}$) and growth (t_{40}) in an attempt to find out a density-dependent growth history but did not detect any significant relationship between the two parameters.

Discussion

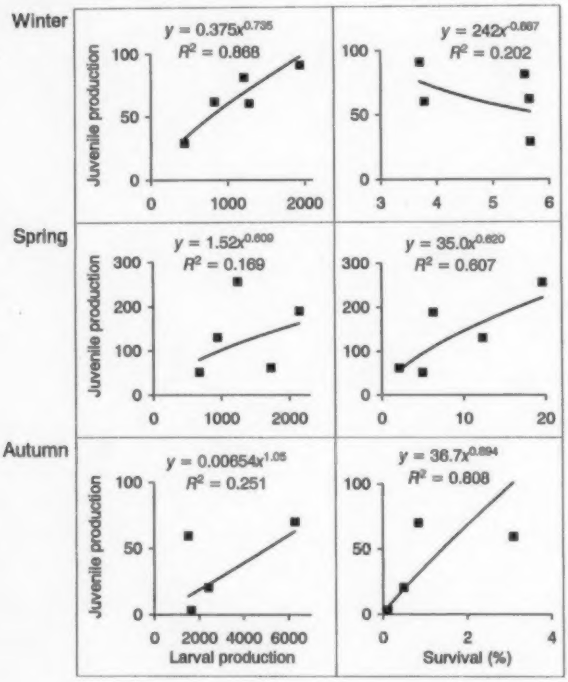
Field samplings

Field sampling in this study was conducted during research cruises to investigate the distribution of various fish species, and as a result, there were constraints in the spatial arrangement over spawning grounds in each season. We did not reach the margin of the spawning grounds during our survey efforts (Fig. 2), and therefore, we cannot delimit the actual spawning ground of the saury in each season. Instead of estimating the total larval production over a distribution area as was done for North Sea herring (*Clupea harengus*) (Heath 1993), we estimated larval and juvenile production in a unit area (per square kilometre). As the sampling stations covered the temperature zones suitable for saury spawning (15–21°C) (Fig. 2) in the most active spawning months in each season, October and (or) November in autumn, February in winter, and May and June in spring (Watanabe and Lo 1989), the estimates should be representative of the parameters in the larval and early juvenile stages of the saury in each season. Sampling stations were nearly evenly distributed in winter and spring over the survey area but were coastal-weighted in autumn (Fig. 2). Because we did not use a statistical stratification procedure in this study, the estimates in the autumn spawning season could be overrepresented in the coastal waters. The data in winter and autumn 1990 and winter 1993 may be less precise because of smaller numbers of tow samples distributed in the extensive spawning area.

Larval production

Daily larval production at the hatching size-class ($P_{t_{7.9}}$) was highest in autumn among the three seasons in the years studied. Spawning of the saury is considered to have been most active in autumn in the mixed-water region between the Oyashio front and the Kuroshio Extension during the 1990's. Watanabe and Lo (1989) summarized larval catch data during 1973–1986 and demonstrated that winter was the most active spawning season for saury preceded by the early (autumn) and followed by the late (spring) spawning seasons. Sauries in the large and extra-large size-classes made up 70.8 ± 14.8% of the total catch (in number of sauries) landed during the 1990's, while the proportion was 42.9 ± 18.4% during 1973–1986 (Tohoku National Fisheries Research Institute 1995). Peak spawning

Fig. 4. Regressions of preschooling juvenile production ($km^{-2} \cdot d^{-1}$) on larval production ($km^{-2} \cdot d^{-1}$) in the hatching size-class (left panels) and on overall percent survival (right panels). The regression equation and the coefficient of determination (R^2) are shown at the top of each panel.



has shifted from winter to autumn during the 1990's and has resulted in a relative increase in the large and extra-large size-classes of sauries.

Growth

Growth rates of saury in the 14 cohorts studied, t_{40}= 45.3–76.2 d, were slower than that estimated from larvae and juveniles collected in the northwestern Pacific in 1984 and 1985 (Watanabe et al. 1988). We recalculated the Gompertz curve from their data on sizes-at-age of larvae and juveniles up to 63.5 mm KnL (largest juvenile specimen in the current study). Sauries became 40-mm preschooling juveniles in 37.6 d during the mid–1980's (L_{inf}= 70.0 mm, K = 0.0502, t_f= 26.1, N = 37, Var = 41.8). Daily larval production ($P_{t_{79}}$) calculated from Watanabe and Lo (1989) in 1984 and 1985 was 402 and 124·$km^{-2} \cdot d^{-1}$, respectively. Larval production during the 1990's presented in this paper ($P_{t_{79}}$ = 434–6287·$km^{-2} \cdot d^{-1}$) was higher than that during the mid–1980's. High larval production might have resulted in slow growth through density-dependent processes such as competition for food (Shepherd and Cushing 1980; Jenkins et al. 1991). As far as the current data set for the 1990's is concerned, we did not detect any significant relationship between larval production and growth.

Juvenile sauries become more agile and may have higher potential for evading net mouth openings than larvae. The decline in catch efficiencies of juvenile sauries using a similar type of 1.3-m-diameter net in daytime (Watanabe and Lo 1989) is indicative of this possibility. There would be a growth rate related bias in the sampling method in this paper, i.e., juveniles with higher growth rate are larger than those with slower growth rates at the same age and have lower vulnerability to net tow sampling. We corrected the number of fish in a sample collected at a certain time of day by time-of-day and size-dependent correction factors for catch efficiency to estimate fish abundance in size categories. To estimate a growth curve, however, a correction of this kind is not possible for the current data set. Whether or not such a growth rate related sampling bias of juveniles exists for the net sampling method in this study should be examined by comparing growth curves in the current paper and those estimated from different methods of fish collection, i.e., a large neuston net with less net evasion by larger fish.

Saury larvae and juveniles grew fastest in winter among the three spawning seasons. Major food items of saury larvae and juveniles are copepod nauplii and small copepod species (K. Odate 1977). Nakata et al. (1995) calculated that production of nauplii and copepods <1.0 mm prosomal length exceeded by nine times the total food requirements of carnivorous macrozoolankters and Japanese sardine (*Sardinops melanostictus*) larvae in the waters along the Kuroshio Current in March. Clearly, these waters provide sardine and saury larvae with a habitat with high food availability. This is supported by the fact that percent survival of the Japanese sardine from egg to the end of the first feeding stage in February and March improved with the expansion of spawning grounds toward the Kuroshio Current axis (Watanabe et al. 1996) and that the majority of first-feeding larvae of the sardine in the Kuroshio waters in February had high RNA/DNA ratios indicative of healthy conditions (Kimura et al. 1996).

As for the waters offshore of the Kuroshio where a large proportion of larval and juvenile sauries were distributed, Nakata et al. (1995) also calculated that small copepod production in the waters made up 73% of the total requirements of their predators. However, they did not include saury larvae and juveniles as predators on small copepods in their calculations. If sauries had been included, the percentage of prey production would have been lower. The low food availability for larvae in offshore waters reduced the nutritional condition of Japanese sardine larvae (Hayashi et al. 1994). Saury larvae start continuous swimming against a mild current upon hatching and start feeding within 1–2 d (Watanabe and Kuji 1991). They are assumed to have a better ability to search and capture food items than sardine larvae. The small variance in t_{40} in winter indicates that even in the waters offshore of the Kuroshio, saury larvae and juveniles grow as fast as those in the waters along the Kuroshio. Sea surface temperatures were 20–22°C in the offshore waters. High temperature could be advantageous for saury larvae and juveniles with a high feeding potential to grow as fast as 0.99 mm·d^{-1} (Table 3).

During the spring spawning season in the mixed-water region, the total zooplankton biomass is much higher than that in the Kuroshio waters in winter (Odate 1994). However, this high food availability could be cancelled out by the low temperature (Hewitt et al. 1985), as shown by older age at length 40 mm in spring. In the mixed-water region in autumn, zooplankton biomass is lower than in spring (Odate 1994) and the temperature is lower than in winter (Fig. 2), which seems to have resulted in the lowest growth rates in the autumn cohort.

Mortality

Daily mortality coefficients were highest in the autumn- and lowest in the spring-spawned cohorts (Table 4). This to some extent coincides with the difference in zooplankton biomass between the waters as described above. High mortality in the juvenile stage during winter is possible for the autumn cohort. Autumn-spawned sauries are thought to migrate south into the Kuroshio Extension and overwinter in the waters far from the Japanese coast (S. Odate 1977). Due to large interannual variability in environments in the oceanic frontal area between the Kuroshio Extension and the mixed-water region (Kawai 1982), high mortality may occur in autumn-spawned juveniles during winter.

Southward migration of autumn-spawned juvenile sauries may have introduced a bias in our estimation. If some proportion of juveniles <45 mm start southward migration in late autumn with a decline of sea surface temperature, apparent high mortality rates of the autumn cohort may partly be due to their emigration from our survey area. An opposite situation is possible for the spring cohort. Winter-spawned sauries migrate north from the Kuroshio waters to the mixed-water region in spring, with a rise in water temperature (S. Odate 1977). Sauries spawned in late winter, i.e., in March, might appear in the mixed-water region in spring as juveniles <45 mm and inflate our abundance estimates for juveniles in spring. Low coefficients of determination of mortality curves in spring, $R^2 = 0.73–0.95$ (Table 4), might have been the result of some immigration of winter-spawned juveniles.

Parameters determining juvenile production

Large variances in growth and mortality resulted in variable preschooling juvenile production in spring (CV = 62.2%) and autumn (81.8%) cohorts. Oceanic environments on the spawning grounds in the mixed-water region are variable owing to interactions between the Oyashio and Kuroshio. Interannual latitudinal shifts of the Oyashio front (Hirai and Yasuda 1988; Yasuda and Watanabe 1994) and the Kuroshio Extension (Kawai 1982) and the development and evolution of warm core rings (Yasuda et al. 1992) caused wide ranges in temperature in the mixed-water region (Fig. 2). The large variations in growth, mortality, and fish production in the mixed-water region are assumed to stem from variable environmental conditions.

Overall percent survival up to preschooling juveniles of 40 mm KnL in autumn 1990 was 0.11%, lower by 2 orders of magnitude than the 19.7% in spring 1990 (Table 4). In spite of the highest spawning activity, average production of preschooling juveniles in autumn was minimal because of the cumulative effects of a high mortality coefficient ($Z = 0.104 \pm 0.023$) operating over longer time duration ($t_{40} = 59.4 \pm 12.7$ d) due to slow growth. In the mortality curves established in this study, no critical mass mortality was detected at a particular period in the larval or juvenile stages. However, order-of-magnitude differences in percent survival occurred between the spawning seasons. Chronic effects of growth and mortality rates in the larval and preschooling juvenile stages determined overall percent survival, and therefore, eventual production of preschooling juveniles as theoretically pointed out by Houde (1989).

In winter, variation in preschooling juvenile production (CV = 36.7%) was smaller than that in larval production in the hatching size-class (49.4%). The reduction in variance with ageing might imply the presence of density-dependent processes stabilizing the population of a cohort. van der Veer and Bergman (1987) demonstrated that the CV in the abundance of newly settled plaice (*Pleuronectes platessa*) in the Dutch Wadden Sea was 62–69% during 1973–1982, while after the period of predation by crustaceans from April to June, it dropped to 35%. They considered this drop to be due to density-dependent regulation of the age–0 group plaice population by predation mortality. In the case of saury in the winter spawning season, however, a correlation was not found between percent survival and larval production (Table 4). Density-dependent negative feedback could not be detected in the current 5-yr data set.

Production of preschooling juveniles was determined differently among the spawning seasons (Fig. 4). Under stable environmental conditions along and offshore of the Kuroshio in winter, juvenile production ($P_{t_{40}}$) was determined by larval production ($P_{t_{7.9}}$). Juvenile production was directly linked to larval production with slight modifications by cumulative mortality through the larval and juvenile stages. However, in the mixed-water region in spring and autumn, although not statistically significant, juvenile production could be better explained by overall percent survival than by larval production. Larval production was largely modified by variable overall survival in juvenile sauries through early life stages under variable environmental conditions.

Juvenile production was highest in spring ($P_{t_{40}} = 138.6 \pm 86.3$ km^{-2} d^{-1}). However, the percentage of landings from the fishery in the young and small size-classes was usually small (Table 1), and more than 70% of sauries landed during the 1990's were from large and extra-large size-classes (Tohoku National Fisheries Research Institute 1995). This seems to be due to strong selectivity for large fish by fishing fleets. When using stick held dip nets, fishers lure sauries by intense lights at night and scoop up a dense shoal of fish gathering around the fishing boat. When they see that a large proportion of fish are small, they do not operate a scoop net because of the low commercial profitability.

Stable juvenile production in winter seems to be linked to stable percent catch in number of sauries of medium size (Table 1). Variable juvenile production in autumn and spring is thought to reflect large interannual variations in percent catch in number of large and small sauries. Fukushima et al. (1990) demonstrated from data collected during 1949–1975 that interannual variations in larval and juvenile abundance were large in spring and autumn, compared with relatively stable abundance in winter, which resulted in large annual fluctuations in percent landings of small and large fish. Although recruitment forecasting from larval abundance has not been successful (Heath 1992), it might be possible to provide a recruitment forecast for the saury population based on production of preschooling juveniles. The short time from the preschooling juvenile stage to recruitment to the fishery (6–10 mo) in the saury (Watanabe et al. 1988) seems to be advantageous in providing a forecast.

Acknowledgments

We thank N.C.H. Lo and M. Heath for their constructive comments in improving the manuscript. Specimens of larval and juvenile sauries were collected by Prefectural Fisheries Experimental Stations in Hokkaido, Iwate, Miyagi, Fukushima, Ibaraki, Chiba, and Shizuoka and Tohoku and Nansei National Fisheries Research Institutes and National Research Institute of Fisheries Science with financial support by the Japan Fishery Agency. H. Furukawa, K. Takahashi, and K. Asakura read the otoliths. We used the sea surface temperarure data compiled by D. Inagake and Y. Shimizu. T. Akamine provided us with computation programs of the Gompertz and logistic growth model fittings.

References

Akamine, T. 1986. Expansion of growth curves using a periodic function and BASIC programs by Marquardt's method. Bull. Jpn. Sea Reg. Fish. Res. Lab. **36**: 77–107.

Fukushima, S., Watanabe, Y., and Ogawa, Y. 1990. Correspondence of spawned seasons to large, medium, and small size Pacific saury exploited in the northwestern Pacific Ocean. Bull. Tohoku Natl. Fish. Res. Inst. **52**: 17–27.

Hayashi, A., Tsuruta, Y., and Kawaguchi, K. 1994. Nutritional conditions of Japanese sardine larvae in the Kuroshio and its adjacent waters. Bull. Jpn. Soc. Fish. Oceanogr. **58**: 145–152.

Heath, M. 1992. Field investigations of the early life stages of marine fish. Adv. Mar. Biol. **28**: 1–174.

Heath, M. 1993. An evaluation and review of the ICES herring larval surveys in the North Sea and adjacent waters. Bull. Mar. Sci. **53**: 795–817.

Hewitt, R.P., Theilacker, G.H., and Lo, N.C.H. 1985. Causes of mortality in young jack mackerel. Mar. Ecol. Prog. Ser. **26**: 1–10.

Hirai, M., and Yasuda, I. 1988. Interannual variability of the temperature field at 100 m depth near the east coast of Japan. Bull. Ohzuchi Ocean Res. Cent. Univ. Tokyo, **14**: 184–186.

Houde, E.D. 1989. Subtleties and episodes in the early life of fishes. J. Fish Biol. **35**(Suppl. A): 29–38.

Japan Saury Fishery Association. 1995. Data of saury fishery in 1994. No. 33. pp. 1–42.

Jenkins, G.P., Young, J.W., and Davis, T.L.D. 1991. Density dependence of larval growth of marine fish, the southern bluefin tuna, *Thunnus maccoyii*. Can. J. Fish. Aquat. Sci. **48**: 1358–1363.

Kawai, H. 1982. Hydrography of the Kuroshio Extension. *In* Kuroshio. *Edited by* H. Stommel and K. Yoshida. University of Tokyo Press, Tokyo. pp. 235–352.

Kimura, K. 1956. The standard length of the Pacific saury, *Cololabis saira* (Brevoort). Bull. Tohoku Reg. Fish Res. Lab. **7**: 1–11.

Kimura, R., Sato, C., and Nakata, K. 1996. Nutritional condition of first-feeding larvae of sardine *Sardinops melanostictus*. *In* Survival strategies in early life stages of marine resources. *Edited by* Y. Watanabe, Y. Yamashita, and Y. Oozeki. A.A. Balkema, Rotterdam, The Netherlands. pp. 105–113.

Matsumiya, Y., and Tanaka, S. 1978. Dynamics of the saury population in the Pacific Ocean off northern Japan — III. Reproductive relations of large and medium sized fish. Bull. Jpn. Soc. Sci. Fish. **44**: 451–455.

Nakata, K., Zenitani, H., and Inagake, D. 1995. Differences in food availability for Japanese sardine larvae between the frontal region and the waters on the offshore side of Kuroshio. Fish. Oceanogr. **4**: 68–79.

Odate, K. 1977. On the feeding habits of the Pacific saury, *Cololabis saira* (Brevoort). Bull. Tohoku Reg. Fish. Res. Lab. **38**: 75–88.

Odate, K. 1994. Zooplankton biomass and its long-term variation in the western North Pacific Ocean, Tohoku Sea area, Japan. Bull. Tohoku Natl. Fish. Res. Inst. **56**: 115–173.

Odate, S. 1977. On the distribution of Pacific saury in the North Pacific Ocean. Res. Inst. North Pac. Fish. Sp. Vol. X. Faculty of Fisheries, Hokkaido University, Hakodate, Japan. pp. 353–382.

Odate, S., and Hayashi, K. 1977. Ecological studies on the larvae and juveniles of the Pacific saury, *Cololabis saira* (Brevoort). Bull. Tohoku Reg. Fish. Res. Lab. **38**: 89–101.

Oozeki, Y., Watanabe, Y., Kuji, Y., and Takahashi, S. 1991. Effects of various preservatives on the body length of saury larvae. Bull. Tohoku Natl. Fish. Res. Inst. **53**: 15–21.

Shepherd, J.G., and Cushing, D.H. 1980. A mechanism for density dependent survival of larval fish as the basis for a stock–recruitment relationship. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **39**: 160–167.

Smith, P.E., and Richardson, S.L. 1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Pap. **175**: 1–100.

Tohoku National Fisheries Research Institute. 1995. Annual report of the research meeting on saury resources No. 43. Tohoku National Fisheries Research Institute, Japan.

van der Veer, H.W., and Bergman, M.J.N. 1987. Predation by crustaceans on a newly settled 0-group plaice *Pleuronectes platessa* population in the western Wadden Sea. Mar. Ecol. Prog. Ser. **35**: 203–215.

Watanabe, Y. 1990. A set of brightness categories for examining diel change of catch efficiency of saury larvae and juveniles by a neuston net. Bull. Jpn. Soc. Fish. Oceanogr. **54**: 237–241.

Watanabe, Y., and Kuji, Y. 1991. Verification of daily growth increment formation in saury otoliths by rearing larvae from hatching. Jpn. J. Ichthyol. **38**: 1–15.

Watanabe, Y., and Lo, N.C.H. 1989. Larval production and mortality of Pacific saury, *Cololabis saira*, in the northwestern Pacific Ocean. Fish. Bull. U.S. **87**: 601–613.

Watanabe, Y., Butler, J.L., and Mori, T. 1988. Growth of Pacific saury, *Cololabis saira*, in the northeastern and northwestern Pacific Ocean. Fish. Bull. U.S. **86**: 489–498.

Watanabe, Y., Zenitani, H., and Kimura, R. 1996. Offshore expansion of spawning of the Japanese sardine, *Sardinops melanostictus*, and its implication for egg and larval survival. Can. J. Fish. Aquat. Sci. **53**: 55–61.

Yasuda, I., and Watanabe, Y. 1994. On the relationship between the Oyashio front and saury fishing grounds in the north-western Pacific: a forecasting method for fishing ground locations. Fish. Oceanogr. **3**: 172–181.

Yasuda, I., Okuda, K., and Hirai, M. 1992. Evolution of a Kuroshio warm-core ring: variability of the hydrographic structure. Deep-Sea Res. **39**(Suppl.): S131–S161.

Sex-specific temperature distribution of American plaice (*Hippoglossoides platessoides*) and its relation to age and abundance

Douglas P. Swain

Abstract: I examined variation in the temperature distribution of American plaice (*Hippoglossoides platessoides)* in the southern Gulf of St. Lawrence using data from bottom trawl surveys conducted each September since 1971. Plaice tended to select cold temperatures relative to those available. Temperature distribution was unrelated to age over the range 3–12$^+$ years. Females tended to occupy warmer water than males, although the extent of this difference between the sexes varied among years. Annual variation in plaice temperature distribution was positively correlated with variation in the temperatures available. After accounting for annual variation in available temperatures, female temperature distribution was density independent but males tended to occupy colder water at higher levels of abundance. The median temperature occupied by both sexes tended to be warmer at higher levels of abundance of Atlantic cod (*Gadus morhua*), a competitor of plaice. The difference between the sexes in temperature distribution increased as cod abundance decreased or as plaice abundance increased (depending on the measure of temperature distribution used). The observed difference between the sexes in temperature distribution and its density dependence may reflect differences in foraging rate associated with differences between the sexes in the fitness benefits of growth.

Résumé : J'ai examiné la variation dans la distribution de la plie canadienne (*Hippoglossoides platessoides*), en fonction de la température dans le sud du golfe du Saint-Laurent à l'aide des données tirées de relevés par chalutage de fond réalisés tous les mois de septembre depuis 1971. Les plies avaient tendance à choisir des températures froides parmi celles qui étaient disponibles. La distribution en fonction de la température n'était pas liée à l'âge dans l'étendue d'âges 3 à 12$^+$ a. Les femelles avaient tendance à fréquenter des eaux plus chaudes que les mâles, bien que l'ampleur de cette différence entre les sexes ait varié d'une année à l'autre. La variation annuelle de la distribution de la plie en fonction de la température était corrélée positivement avec la variation des températures disponibles. Après avoir tenu compte de la variation annuelle dans les températures disponibles, on constate que la distribution des femelles en fonction de la température était indépendante de la densité, mais que les mâles avaient tendance à fréquenter les eaux plus froides à des degrés d'abondance plus élevés. La température médiane occupée par les deux sexes avait tendance à être plus chaude lorsque les degrés d'abondance de la morue franche (*Gadus morhua*), un compétiteur de la plie, sont plus élevés. La différence entre les deux sexes en ce qui a trait à la distribution en fonction de la température a augmenté avec la diminution de l'abondance de la morue ou avec l'augmentation de celle de la plie (selon la mesure utilisée de distribution en fonction de la température). La différence observée entre les sexes dans la distribution en fonction de la température et sa dépendance à l'égard de la densité peuvent refléter des différences dans les taux de broutage liés à des différences entre les sexes pour ce qui est des avantages de la croissance du point du vue de «fitness».
[Traduit par la Rédaction]

Introduction

Temperature is a key environmental factor for fishes (e.g., Fry 1971; Reynolds and Casterlin 1979*b*), controlling the rates of physiological processes such as metabolism and affecting many components of fitness such as growth rate (e.g., Brett 1971; Magnuson et al. 1979). Most fishes occupy a limited range of preferred temperatures, and numerous studies have reported relationships between temperature and the spatial distribution of fishes (e.g., Scott 1982; Mahon et al. 1984; Rose and Leggett 1988; Sinclair 1992). However, fish distribution is not likely to be determined solely by physical factors such as temperature. Biotic factors such as prey abundance are also important determinants of habitat quality. For example, Rose and Leggett (1989) concluded that distribution patterns of Atlantic cod (*Gadus morhua*) were determined by interactive effects of temperature and food resources, and Swain (1993) suggested that changes in cod distribution reflected a trade-off between density-dependent effects associated with food resources and density-independent costs associated with temperature.

Growth rate of fishes is affected by an interaction between temperature and food ration. As ration decreases, so does the temperature yielding the highest growth rate (Brett et al. 1969; Elliott 1975; Woiwode and Adelman 1991). This relationship reflects reduced metabolic costs at lower temperatures. Thus, if fish select habitats that yield the highest growth rates, then preferred temperature should decrease as food rations decrease (Elliott 1979; Crowder and Magnuson 1983). In laboratory tests, fish do tend to occupy colder temperatures on reduced rations, but the change in temperature distribution is generally small and less than that required to maximize growth

Received April 10, 1996. Accepted October 10, 1996.
J13398

D.P. Swain. Department of Fisheries and Oceans, Gulf Fisheries Centre, P.O. Box 5030, Moncton, NB E1C 9B6, Canada. e-mail: swaind@gfc.dfo.ca

Can. J. Fish. Aquat. Sci. **54**: 1077–1087 (1997)

(e.g., Javaid and Anderson 1967; Stuntz and Magnuson 1976; Reynolds and Casterlin 1979*a*; Mac 1985; Boltz et al. 1987; Wildhaber and Crowder 1990; Morgan 1993). The only available field test also provides qualitative support for the prediction of an inverse relationship between food supply and preferred temperature. Swain and Kramer (1995) reported that cod in the southern Gulf of St. Lawrence tended to occupy colder temperatures during the feeding season in years of higher abundance (when per capita food intake may have been reduced).

Ontogenetic effects on thermal preference appear to be common in fishes, with younger fish preferring warmer temperatures. In laboratory tests, preferred temperature decreased with age in yellow perch (*Perca flavescens*) (McCauley and Read 1973), alewife (*Alosa pseudoharengus*) (Otto et al. 1976), yellow bullhead (*Ictalurus natalis*) (Reynolds and Casterlin 1978), and rainbow trout (*Oncorhynchus mykiss*, previously *Salmo gairdneri*) (Kwain and McCauley 1978) but was unrelated to age in largemouth bass (*Micropterus salmoides*) (Reynolds et al. 1976). In the field, the temperatures occupied by cod decreased with age during the summer and fall feeding season in the Gulf of St. Lawrence (Tremblay and Sinclair 1985; Swain and Kramer 1995) and on the Scotian Shelf (Sinclair 1992) but increased with age in the Barents Sea in winter (Nakken and Raknes 1987). Macpherson and Duarte (1991) suggested that the widespread trend for demersal fish size to increase with depth may reflect a tendency for larger (older) fish to prefer colder water.

In many animals the sexes differ in size at a given age. One possible cause of such differences is a difference between the sexes in foraging rate (e.g., Holtby and Healey 1990). Thus, because of the link between food ration and the optimum temperature for growth, differences in temperature preference might be expected between the sexes in species with sexually dimorphic growth rates, with the sex with the higher growth rate preferring warmer temperatures. Tests for a difference between the sexes in temperature preference appear to be rare. Males are less resistant than females to high temperatures in the poeciliid *Gambusia affinus* (Hagen 1964) and in the cyprinid *Dionda nubila* (Baker et al. 1970) and to low temperature in guppy (*Poecilia reticulata*) (Fujio et al. 1990). In laboratory tests, male guppies preferred a lower temperature than females or juveniles (Johansen and Cross 1980). This difference appeared to be caused by the male androgenic hormone testosterone; treatment with testosterone lowered the preferred temperature of females and juveniles to that of males.

In this paper, I examine variation in the temperature distribution of American plaice (*Hippoglossoides platessoides*) during the feeding season in the southern Gulf of St. Lawrence over a 24-year period. I test for temperature selection by plaice, comparing the temperatures occupied with those available. I also test for ontogenetic effects on plaice temperature distribution and test whether annual variation in the temperature distribution of plaice is related to plaice population size or variation in environmental conditions. Finally, because growth rate is sexually dimorphic in plaice, with females growing at a faster rate than males (e.g., Powles 1965; R. Morin, Department of Fisheries and Oceans, Moncton, N.B., personal communication), I tested for an effect of sex on the temperature distribution of plaice.

Material and methods

Study area and population

The southern Gulf of St. Lawrence consists of a shallow shelf, the Magdalen Shallows, with depths less than 100 m, bordered by a 500-m trench, the Laurentian Channel (Fig. 1). In summer and fall, three water layers are present in the southern Gulf: a deep warm (4–6°C) layer along the edge of the Laurentian Channel, a cold (–1 to 2°C) intermediate layer underlying the thermocline, and a warm mixed layer above the thermocline. The cold intermediate layer covers the bottom over much of the Magdalen Shallows, with bottom temperatures increasing shoreward as depth decreases and towards the Laurentian Channel as depth increases (see Fig. 2 in Swain and Kramer (1995) or Fig. 21 in Gilbert et al. (1996)). In winter, the area is typically ice-covered, and water temperatures are near the freezing point (–1.5°C) from the surface to the deep warm layer.

Plaice occupy feeding grounds on the Magdalen Shallows from May to October and then migrate offshore to overwintering grounds in the warm deep water along the Laurentian Channel (Powles 1965). Two groups of plaice occur on the Shallows in summer: a northwestern group occupying Chaleur Bay and the Orphan Bank areas and a southeastern group concentrated along the Cape Breton coast (Powles 1965; Swain and Morin 1996). Although adult plaice tend to return to the same area each year (Powles 1965), the two groups appear to comprise a single population (Powles 1965; Stott et al. 1992; Swain and Morin 1996). Females grow at a faster rate and mature at a larger size and older age than males (Powles 1965; R. Morin, personal communication). Abundance of plaice in the southern Gulf has varied fivefold since 1971 (Morin and Sinclair 1993). Abundance was high from 1974 to 1981 but has remained low since then (Fig. 2).

Data sources

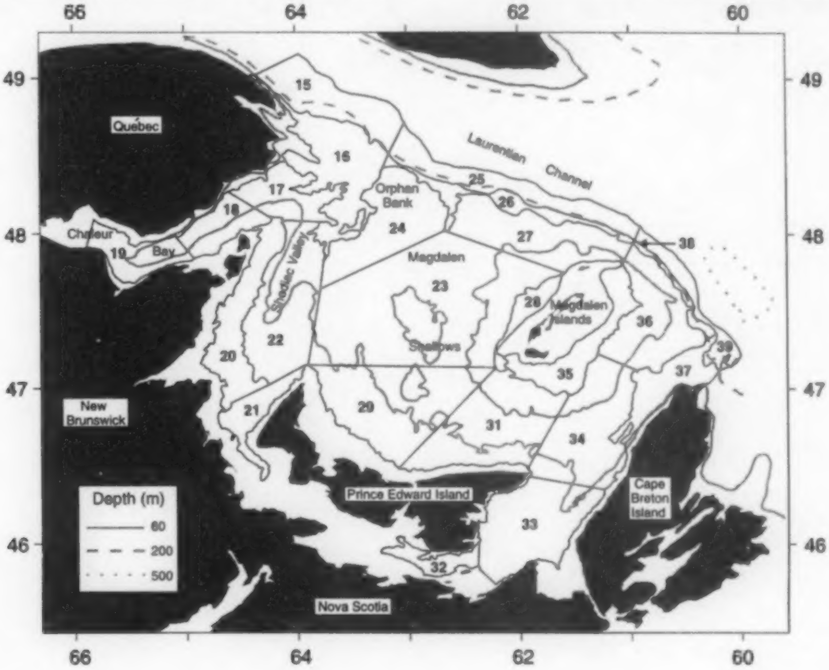
I estimated near-bottom temperature and the distribution of plaice in relation to temperature from bottom trawl surveys conducted in the southern Gulf each September since 1971. Surveys used a stratified random design, with stratification based on depth and geographic region (Fig. 1). Survey procedures are described in Hurlbut and Clay (1990) and summarized in Swain and Wade (1993). For each trawl tow, plaice catch was estimated for each sex and each age from 3 to 12^+ years (i.e., 12 years and older) as described by Swain and Morin (1996*a*). Catches were adjusted to a standard tow of 1.75 nautical miles. Because the sexes were not sampled separately in 1984–1986, these three years are omitted from the analyses presented here.

Near-bottom temperature was measured after each trawl tow using reversing thermometers and mechanical bathythermographs (MBTs) in 1971–1983, MBTs in 1987 and 1988, an electronic bathythermograph (Femto model 8720) in 1989 and 1990, and a Seabird SBE-19 profiler since 1991. The MBTs used in 1987 and 1988 permitted temperature measurements only to a depth of 145 m. Tows at depths greater than 155 m were omitted from analyses in all years so that results would be comparable among years. Six strata had a high proportion of tows at depths greater than 155 m and were omitted from analyses (strata 15, 25, 26, 37, 38, and 39; 14% of the survey area; Fig. 1). Plaice tended to be rare in these deep strata; estimated plaice biomass in these strata was on average 2% of the survey total in 1971–1994 (median 1.6%, minimum 0.4%, maximum 5.9%). After omitting these strata and deep tows, sample sizes averaged 55 tows per year in 1971–1988 (median 52, minimum 41, maximum 99) and 136 tows per year in 1989–1994 (median 132, minimum 115, maximum 156).

Temperature distribution

Following Perry and Smith (1994), I examined relationships between plaice density and temperature using cumulative distribution functions (cdfs). I calculated the cdf (percent) for temperature for each year as follows:

Fig. 1. Map of the southern Gulf of St. Lawrence showing bathymetry and strata used in the September bottom trawl surveys.


66
64
62
60
49
48
47
46
Quebec
Chaleur
Bay
New Brunswick
Prince Edward Island
Nova Scotia
Cape Breton Island
Laurentian Channel
Orphan Bank
Shediac Valley
Magdalen Shallows
Magdalen Islands
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
31
32
33
34
35
36
37
38
39
Depth (m)
60
200
500

(1) $$f(t) = 100\sum_{h=1}^{L}\sum_{i=1}^{n_h}\frac{W_h}{n_h}I \quad \text{where} \quad I = \begin{cases}1, \text{ if } x_{hi} \le t\\ 0, \text{ otherwise}\end{cases}$$

where t is a level of temperature, W_h is the proportion of the survey area in stratum h, n_h is the number of trawl tows in stratum h, x_{hi} is the bottom temperature at the end of tow i in stratum h, and L is the number of strata. I similarly calculated the cdf for plaice catch in relation to temperature for each year:

(2) $$g(t) = 100\sum_{h=1}^{L}\sum_{i=1}^{n_h}\frac{W_h}{n_h}\frac{y_{hi}}{\bar{Y}}I \quad \text{where} \quad I = \begin{cases}1, \text{ if } x_{hi} \le t\\ 0, \text{ otherwise}\end{cases}$$

where y_{hi} is the number of plaice caught in tow i in stratum h and $\bar{Y}$ is the stratified mean catch per tow. I calculated $g(t)$ separately for each sex for age classes 3–12$^+$ and 3$^+$. Using $g(t)$, I calculated the median temperature occupied by plaice and the temperature limits of plaice distribution. Following Rose and Leggett (1988, 1989), I defined these limits as the range of temperatures within which 95% of plaice occurred (i.e., the 2.5th and 97.5th percentiles of $g(t)$). Using $f(t)$, I calculated the median temperature available to plaice and the limits of available temperature (i.e., the 2.5th and 97.5th percentiles of $f(t)$). I also calculated the average temperature available each year:

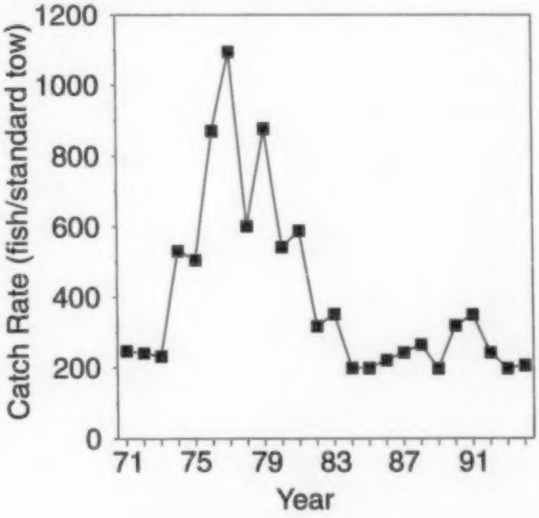
(3) $$T_{\mathrm{AV}} = \sum_{h=1}^{L}\sum_{i=1}^{n_h}\frac{W_h}{n_h}x_{hi}$$

and the average temperature occupied by plaice:

(4) $$P_{\mathrm{AV}} = \sum_{h=1}^{L}\sum_{i=1}^{n_h}\frac{W_h}{n_h}\frac{y_{hi}}{\bar{Y}}x_{hi}$$

I tested variation in plaice temperature distribution using ANOVA with sex, age, and their interaction as fixed effects and year and its interactions with sex and age as random effects (Table 1). These tests were calculated using the GLM procedure of SAS (SAS Institute Inc. 1990).

Fig. 2. Relative abundance of plaice aged 3$^+$ years in the southern Gulf of St. Lawrence, 1971–1994. Catch rate is the stratified mean catch per standard tow in the September survey.



For each year from 1971 to 1994, I tested differences between the sexes in temperature distribution using randomization tests (Edgington 1987). The test statistic was the absolute value of the difference between the average temperature occupied by 3$^+$ females and that occupied by 3$^+$ males. First, I calculated the test statistic for the observed

Table 1. Expected mean squares and tests of significance for the linear model with sex (S), age (A), and their interaction as fixed effects and year (Y) and its interactions as random effects.

Source	Mean square	Type III expected mean square	*F*-test denominator	*F*-test df
Sex	MS_S	$\sigma^2 + 10\sigma^2_{SY} + Q(S,SA)$	MS_{SY}	1,20
Age	MS_A	$\sigma^2 + 2\sigma^2_{AY} + Q(A,SA)$	MS_{AY}	9,180
Year	MS_Y	$\sigma^2 + 2\sigma^2_{AY} + 10\sigma^2_{SY} + 20\sigma^2_Y$	$MS_{SY} + MS_{AY} - MS_{error}$	20,23–34[a]
Sex × age	MS_{SA}	$\sigma^2 + Q(S,A)$	MS_{error}	9,180
Sex × year	MS_{SY}	$\sigma^2 + 10\sigma^2_{SY}$	MS_{error}	20,180
Age × year	MS_{AY}	$\sigma^2 + 2\sigma^2_{AY}$	MS_{error}	180,180

[a] Denominator degrees of freedom, estimated using the Satterthwaite approximation, vary from 23.16 for average temperature to 33.79 for the lower temperature limit.

data for a given year. Then I randomly redistributed plaice catches between sexes. For each tow, one of the observed catches of 3^+ plaice (i.e., male and female) was randomly assigned to males and the other to females. This randomization procedure preserves the observed distribution of plaice with respect to temperature, assuming that differences between the catches of males and females at a particular temperature (i.e., in a particular tow) are due to chance alone. I repeated this randomization 2999 times, calculating the test statistic for each random permutation of the data. I determined N, the number of random permutations with a test statistic equal to or greater than that of the observed data, and calculated $P = (N + 1)/3000$. P is the probability of observing a difference between males and females in temperature distribution as great or greater than that of the observed data under the null hypothesis that differences in the temperature distribution of males and females are due to chance alone.

I examined temperature selection by plaice by comparing the cdfs of temperature and of plaice catch in relation to temperature. For each age–sex class in each year, I calculated

$$(5) \qquad S = \sum_{t=-1}^{20} (f(t) - g(t))$$

where the difference between $f(t)$ and $g(t)$ was summed at 0.5°C intervals from −1.0 to 20.0°C. S compares the average available temperature with the average temperature selected by plaice. Positive values for S indicate selection of relatively warm temperatures compared with those available. Following Perry and Smith (1994), I used a Kolmogorov–Smirnov type of statistic to test the significance of temperature selection. The test statistic D was the maximum absolute vertical distance between $f(t)$ and $g(t)$. Significance was again assessed using randomization tests. In this case, the procedure was to redistribute catches randomly among temperatures for a particular age–sex class in a particular year. I repeated this randomization procedure 2999 times and calculated N and P as described above. In this case, P is the probability of observing a value of D equal to or greater than that of the observed data under the null hypothesis that plaice are randomly distributed in relation to temperature.

I tested effects of annual variation in environmental conditions, plaice abundance, and cod abundance on plaice temperature distribution using linear regression analysis, calculated using the GLM procedure of SAS (SAS Institute Inc. 1990). Cod abundance was included as a predictor of plaice temperature distribution because cod is an important competitor of plaice in the southern Gulf (Powles 1965; J.M. Hanson, Department of Fisheries and Oceans, Moncton, N.B., personal communication). The dependent variable was a measure of 3^+ plaice temperature distribution (mean, median, upper limit, or lower limit), and the independent variables were the corresponding measures of available temperature, relative 3^+ plaice abundance (the stratified mean catch per tow of 3^+ plaice of both sexes), and 3^+ cod abundance (millions of fish at midyear, estimated using sequential population analysis in a recent assessment of this stock in Sinclair et al. 1995). Separate analyses were conducted for male and female plaice. If there is an effect of annual variation in available temperature on plaice temperature distribution, the relationship should be positive (i.e., plaice should be distributed in warmer water in warmer years). Thus, I used one-tailed tests of the effect of available temperature. Similarly, because a negative association between plaice temperature use and abundance is predicted, tests of the effect of plaice abundance were one-tailed. Tests for the effect of cod abundance were two-tailed because its direction was not predicted. (Cod distribution shifts into colder water at higher abundance (Swain and Kramer 1995), so plaice distribution might shift into warmer water to reduce competition with cod or shift into colder water to reduce metabolic costs as ration size decreases because of competition with cod.) I also tested effects of these three independent variables on the difference in temperature distribution between male and female plaice. The dependent variable was the difference between 3^+ females and 3^+ males in either the average temperature occupied or the median temperature occupied (i.e., 3^+ females minus 3^+ males). Tests were all two-tailed because the direction of these effects on the difference in temperature distribution between females and males was not predicted.

Results

Temperature selection

Plaice tended to select cold temperatures relative to those available (see examples in Figs. 3 and 4). The extent and significance of temperature selection varied among years and age–sex classes (Fig. 4). The only year when some age–sex classes of plaice tended to occupy temperatures warmer than the average available was 1971, and in no case was this selection of warm temperatures significant ($P > 0.1$). The difference between plaice temperature distributions and those available tended to be greatest in the 1978–1981 period (Fig. 4). Selection of relatively cold water by plaice tended to be most signficant in the 1989–1993 period. The magnitude of temperature selection (i.e., the absolute value of S) tended to be smaller in the 1989–1993 period than in the 1978–1981 period, so the prevalence of significant results in recent years may partly reflect the increased sample size in recent surveys compared with those in the 1970's and early 1980's. Temperature selection was more often significant ($P < 0.05$) in males and in older plaice. Out of 21 years, temperature selection was significant in one or two years for females aged 3–5 years, in three to seven years for females aged 7–12^+ years, in four to seven years for males aged 3–5 years, and in eight or nine years for males aged 7–12^+ years.

Measures of temperature distribution other than the average lead to similar conclusions (Fig. 5). The median temperature occupied by plaice was colder than the median available for both sexes and all ages from 3 to 12^+ years. Similarly, the upper temperature limit to plaice distribution was considerably lower than the upper limit of available temperature for all

Fig. 3. Cumulative frequency distributions of temperature and of plaice catch in relation to temperature for selected years.

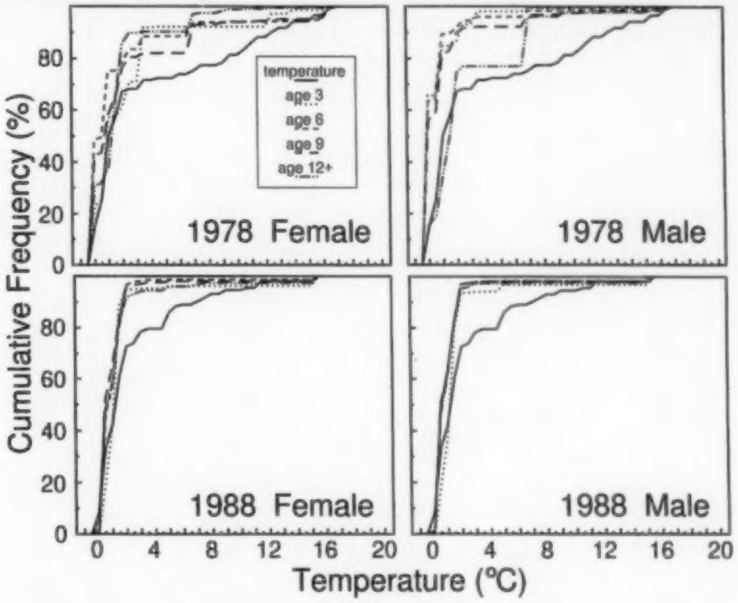
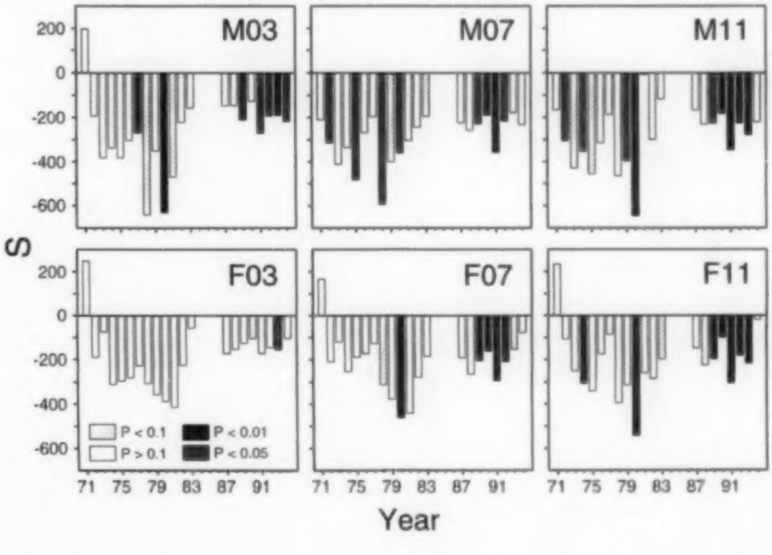


Fig. 4. Index of temperature selection (*S*) by male (M) and female (F) plaice aged 3, 7, and 11 years in the southern Gulf of St. Lawrence in September (no data available for 1984–1986). *S* compares the average temperature occupied by plaice with that available. Negative values indicate selection of relatively cold temperatures by plaice. Shading gives the statistical significance of temperature selection based on the randomization test described in the text.



age–sex classes. The lower temperature limit to plaice distribution was close to the lower limit of available temperature.

Age- and sex-dependent variation in plaice temperature distribution

The linear model with terms for sex, age, year, and their first-order interactions explained 94–99% of the variation in plaice temperature distribution (Table 2). The year term accounted for most of the explained variation. Temperature distribution was, on average, unrelated to age (Table 2; Fig. 5). The age × year interaction was highly significant for all measures of temperature distribution (Table 2), but no obvious pattern is evident for this interaction (Fig. 6). Except for the lower limit to distribution, temperature distribution was on average significantly

Fig. 5. Average temperature distributions in September (1971–1994 period, excluding 1984–1986) in the southern Gulf of St. Lawrence for male and female plaice aged 3, 6, 9, and 12⁺ years compared with the average conditions available (Environ.). Vertical bars show ± 1 SE. Measures of temperature distribution are the stratified average, median, upper limit (97.5th percentile), and lower limit (2.5th percentile).

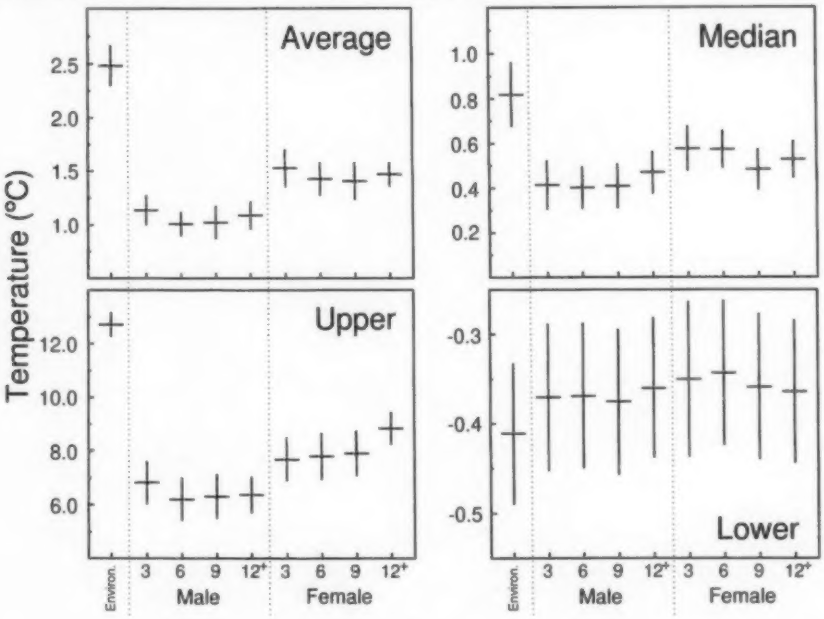


Table 2. Effects of sex, age, and year on plaice temperature distribution.

Source		Average	Median	Upper	Lower
	R^2	0.94	0.95	0.94	0.99
Sex	%SS	7.1	1.4	4.0	0.02
	P	0.001	0.011	0.006	0.41
Age	%SS	0.3	0.2	0.3	0.01
	P	0.86	0.95	0.88	1.00
Year	%SS	65.2	76.9	67.5	96.60
	P	0.0001	0.0001	0.0001	0.0001
Sex × age	%SS	0.0	0.3	0.6	0.03
	P	1.00	0.19	0.066	0.56
Sex × year	%SS	9.5	3.5	8.3	0.49
	P	0.0001	0.0001	0.0001	0.0001
Age × year	%SS	12.3	12.9	13.0	2.13
	P	0.0001	0.0001	0.0001	0.0001

Note: %SS is the Type III sum of squares (SS) for an effect as a percentage of the total SS. *P* is the significance level for an effect according to the *F*-test described in Table 1.

related to sex (Table 2), with females occupying warmer water than males (Fig. 5). This difference between the sexes was unrelated to age (Fig. 5; Table 2: sex × age interaction, $P =$ 0.07–1.0). The effect of sex on temperature distribution differed among years ($P < 0.0001$, Table 2). Except in 1979, differences between the sexes in the lower limit to temperature distribution were negligible compared with annual variation in the lower limit (Fig. 7). For the other measures of temperature distribution, the tendency for females to occupy warmer water than males was strongest in the 1971–1979 period and weakest in the 1980–1983 period, when this tendency was sometimes reversed (Fig. 7; Table 3). The average temperature occupied by females was significantly ($P < 0.05$) warmer than that occupied by males in seven of the nine years in the 1971–1979 period, in no years in the 1980–1983 period ($P > 0.8$ in all four years), and in four of the eight years in the 1987–1994 period (Table 3).

Effects of abundance and thermal regime

Models including 3^+ plaice abundance, 3^+ cod abundance, and a measure of available temperature explained 34–95% of the annual variation in plaice temperature distribution (Table 4). Annual variation in the temperature available accounted for virtually all of the explained annual variation in the lower temperature limit to plaice distribution and for most of the explained variation in the upper limit and in the average temperature occupied. The effect of variation in available temperature was in the predicted positive direction in all cases and was highly significant for all measures of plaice temperature distribution except the median temperature occupied. The effect of variation in available temperature on the median temperature occupied only approached significance in the case of males and accounted for less of the explained variation in this measure of plaice temperature distribution than did the measures of plaice and cod abundance.

The effect of plaice abundance was in the predicted negative direction for all measures of male temperature distribution except for the lower limit but only for the average and median temperatures occupied by females. This effect was significant for both the median and the average temperatures occupied by

Fig. 6. Annual variation in the September temperature distribution of plaice in the southern Gulf of St. Lawrence by age (years). Values are averaged over the two sexes.

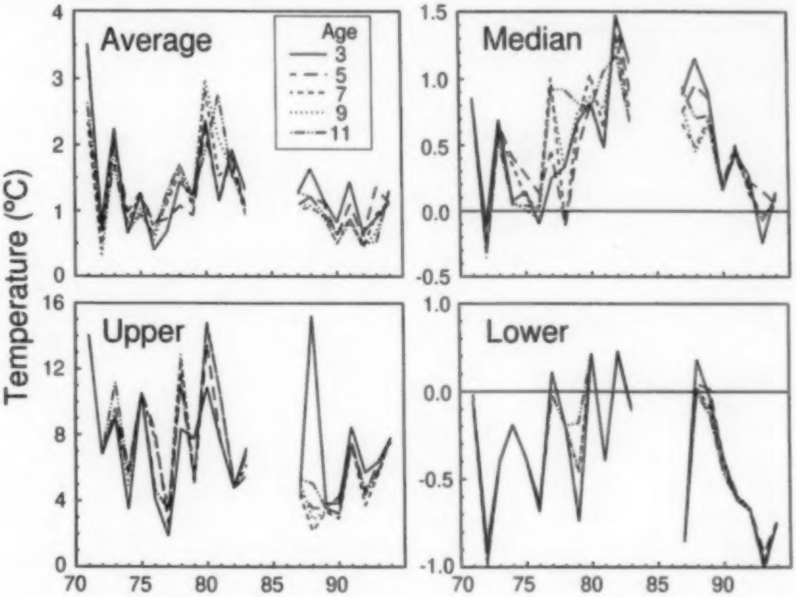
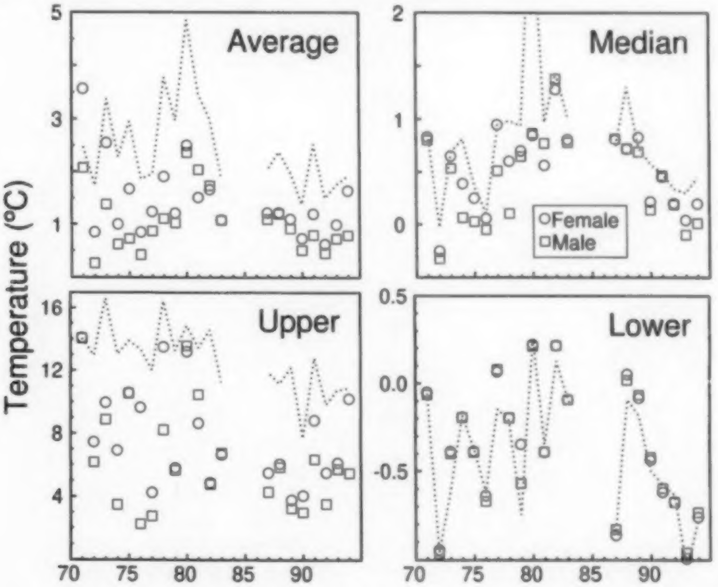


Fig. 7. Annual variation in the September temperature distribution of plaice in the southern Gulf of St. Lawrence by sex. Values are averaged over the 10 age classes from 3 to 12⁺ years. Dotted line shows the available temperature distribution.



males and approached significance for the upper limit to male temperature distribution but did not even approach significance for any measure of female temperature distribution. Cod abundance had a substantial effect on only the median temperature occupied by plaice. This effect was significant for both sexes. In both cases, the median temperature occupied by plaice tended to be warmer when cod abundance was high.

Models including 3^+ plaice abundance, 3^+ cod abundance, and a measure of available temperature explained 28–34% of the annual variation in the difference in temperature distribution between males and females (Table 5). The effect of variation in available temperature was not significant for either measure of this difference. Effects of plaice and cod abundance differed between the two measures of the difference in

Table 3. Randomization tests for differences in temperature distribution between male and female plaice.

Year	ΔT	P
1971	1.320	0.0027
1972	0.457	0.0483
1973	1.172	0.0167
1974	0.337	0.0447
1975	1.029	0.0003
1976	0.373	0.0857
1977	0.302	0.0040
1978	1.114	0.0367
1979	0.159	0.0777
1980	0.095	0.8493
1981	−0.302	0.8053
1982	−0.174	0.8367
1983	0.034	0.8850
1987	0.162	0.0940
1988	0.001	0.9950
1989	0.188	0.0003
1990	0.161	0.0490
1991	0.493	0.0003
1992	0.138	0.1013
1993	0.252	0.0980
1994	0.784	0.0003

Note: ΔT is the test statistic, the average temperature occupied by 3^+ females minus that occupied by 3^+ males. P is the probability that this difference in temperature distribution between males and females is due to chance alone.

temperature distribution. The difference in the average temperature occupied by males and females decreased significantly as cod abundance increased but was unrelated to plaice abundance. The difference between males and females in median temperature occupied increased significantly as plaice abundance increased but was not significantly related to cod abundance.

Discussion

Atlantic cod and American plaice, the two dominant groundfish species in the southern Gulf of St. Lawrence, show contrasting variability in temperature preferences. Temperature preferences of cod during the summer–fall feeding period have varied widely among years, ranging from significant positive selection in some years to significant negative selection in other years (Swain and Kramer 1995). In contrast, temperature preferences of plaice during the feeding season have varied little over the same period, with plaice consistently selecting cold water relative to that available. Several factors may contribute to this difference between the two species. First, cod appear to be thermal generalists whereas plaice appear to be thermal specialists. Cod prefer relatively warm temperatures when food rations are high but may select relatively cold temperatures when rations are low (see discussion in Swain and Kramer 1995). Plaice prefer cold temperatures even when fed high rations (Morgan 1993). Second, variation in plaice abundance over the 1971–1994 period may have been insufficient to produce strong density-dependent shifts in temperature preference. Swain and Kramer (1995) suggested that cod temperature preferences have shifted from warm water at low abundance to cold water at high abundance in order to reduce metabolic costs as abundance increases and food rations decline. Although plaice abundance varied fivefold during the 1971–1994 period, abundance may not have fallen to sufficiently low levels (or food rations risen to sufficiently high levels) to favour incurring the higher metabolic costs of warmer water (see Swain and Morin (1996) for further discussion). Finally, plaice may avoid warm water to avoid competition with cod. However, the plaice preference for relatively cold temperatures even when fed high rations (selecting an average temperature of 1.9°C on a ration of 3% of total body mass twice a week; Morgan 1993) suggests that the lack of wide interannual variation in plaice temperature selection results mainly from thermal specialization to cold temperatures.

This study presents an exception to the tendency for preferred temperature to decrease with age in fishes (e.g., McCauley and Huggins 1979; Sinclair 1992; Swain and Kramer 1995). Although selection of cold water did tend to be significant more often for older plaice, plaice temperature distribution showed no consistent relationship with age over the range 3–12^+ years ($P > 0.85$ for the effect of age on all measures of temperature distribution, Table 2). Previous laboratory tests with freshwater fishes have used very young fish, examining changes in temperature preference during the first year (Kwain and McCauley 1978) or comparing preferences between young-of-the-year and adults (e.g., McCauley and Read 1973). Thus, the contrasting results between these previous studies and the present study on plaice may reflect differences in the range of ages used. Previous studies of the temperature distribution of cod in the wild have compared a wider range of ages than these laboratory studies (e.g., Sinclair 1992; Swain and Kramer 1995). Ontogenetic changes in the temperature distribution of cod were greatest at the youngest ages, but median temperature occupied continued to decline with age up to 5 or 6 years of age. Thus, cod and plaice clearly differ in the effect of ontogeny on temperature preference. No explanation has been proposed for the tendency for preferred temperature to decrease with fish age, except for Macpherson and Duarte's (1991) suggestion that the relationship may involve a trade-off between higher growth rates in warmer water and lower metabolic costs in colder water, so it is premature to speculate on causes of this difference between cod and plaice. One consequence may be the greater spatial segregation among age classes in cod (e.g., Sinclair 1992; Swain 1993) than in plaice (e.g., Walsh 1982; Swain and Morin 1997), resulting in reduced opportunity for cannibalism and competition between age classes in cod compared with plaice (cf. Reynolds and Casterlin 1978) and a greater opportunity for fisheries to target particular age or year classes of cod than of plaice (cf. Sinclair 1992).

For all measures of temperature distribution except the median, the factor explaining the highest proportion of the annual variation in plaice temperature distribution was variation in available temperature. The positive relationships between environmental conditions and plaice temperature distribution indicate that temperature was not closely regulated by plaice (i.e., plaice tended to occur in colder water in colder years). On the other hand, the index of temperature selection by plaice

Table 4. Effects of 3$^+$ plaice abundance (N_P), 3$^+$ cod abundance (N_C), and available temperature (T_A) on the temperature distribution of male and female plaice.

Effect	Statistic	Average	Median	Upper limit	Lower limit
		Male			
	R^2	0.57	0.55	0.34	0.95
N_P	Direction	–	–	–	+
	%SS	8.5	11.2	8.3	0.005
	P	0.042	0.028	0.081	0.55
N_C	Direction	+	+	+	–
	%SS	5.3	14.3	1.2	0.05
	P	0.17	0.033	0.58	0.70
T_A	Direction	+	+	+	+
	%SS	33.8	6.7	28.6	72.1
	P	0.0010	0.066	0.0074	<0.0001
		Female			
	R^2	0.49	0.55	0.41	0.89
N_P	Direction	–	–	+	+
	%SS	4.9	1.0	0.3	1.6
	P	0.11	0.27	0.61	0.93
N_C	Direction	–	+	–	+
	%SS	2.8	12.1	2.7	0.6
	P	0.35	0.048	0.39	0.34
T_A	Direction	+	+	+	+
	%SS	46.4	8.9	37.6	54.3
	P	0.0006	0.043	0.0022	<0.0001

Note: %SS is the Type III sum of squares for an effect as a percentage of the total SS. P is one-tailed for N_P and T_A, and two-tailed for N_C.

Table 5. Effects of 3$^+$ plaice abundance (N_P), 3$^+$ cod abundance (N_C), and available temperature (T_A) on the difference in temperature distribution between female and male plaice (female – male).

Statistic	N_P	N_C	T_A
Average ($R^2 = 0.34$)			
Direction	+	–	+
%SS	0.02	30.5	12.2
P	0.94	0.012	0.094
Median ($R^2 = 0.28$)			
Direction	+	–	–
%SS	25.3	4.1	0.2
P	0.026	0.34	0.84

Note: %SS is the Type III sum of squares for an effect as a percentage of the total SS. P is two-tailed in all cases. T_A is average temperature available in the model testing effects on the difference between males and females in average temperature occupied and median temperature available in the model testing effects on the difference in median temperature occupied.

(S) and thermal regime were negatively correlated (D.P. Swain, unpublished analyses), suggesting that there was some tendency for plaice to regulate their temperature (i.e., to select relatively cold temperatures when conditons were warm, and vice versa). These patterns are similar to those observed for cod in the southern Gulf and would be expected if temperature preferences interact with other factors to determine spatial distribution (Swain and Kramer 1995).

Bioenergetic considerations predict that a decrease in food availability should result in increased use of colder (i.e., less costly) habitats (Elliott 1979; Crowder and Magnuson 1983). The only previous field test supported this prediction: cod in the southern Gulf of St. Lawrence occupied colder temperatures as abundance increased and food ration probably decreased (Swain and Kramer 1995). This study also provides some support for this prediction, although results differed between the sexes. Controlling for variation in available temperature, male plaice did tend to occupy colder water as plaice abundance increased, but female temperature distribution was independent of plaice abundance. However, even for male plaice, density-dependent changes in temperature selection were less striking than for cod. Unlike cod, plaice did not show changes in the *direction* of temperature selection, instead occupying cold water relative to that available at all levels of abundance. Density-dependent temperature selection by male plaice has not resulted in marked changes in either bathymetric pattern (Swain and Morin 1997) or geographic distribution (Swain and Morin 1996) like those displayed by cod in the southern Gulf (Swain 1993; Swain and Wade 1993).

Plaice temperature distribution was significantly sex specific, with females occupying warmer water than males in most years. To my knowledge, this is the first report in fishes of a difference in temperature distribution between males and females in the wild. This difference was not simply a result of the difference in size between the sexes (because temperature distribution was unrelated to age (and thus size) over a wide age and size range). The difference between the sexes in temperature distribution was in the same direction as the difference in preferred temperature reported between male and female guppies in the laboratory (Johansen and Cross 1980). The extent of the difference in temperature distribution between male and female plaice varied from year to year. This may in part reflect the difference between the sexes in the density dependence of temperature distribution. The difference between the sexes in temperature distribution should increase as plaice abundance increases and male distribution shifts to colder water. The significant positive relationship between plaice abundance and the difference between females and males in median temperature occupied is consistent with this expectation.

The difference between male and female plaice in temperature distribution and its density dependence is consistent with an explanation involving sex-specific foraging strategies. Animals commonly face a trade-off between foraging rate and predation risk (e.g., Milinski and Heller 1978; Krebs and Davies 1981; Sih 1982; Gilliam and Fraser 1987; Abrahams and Dill 1989; Holtby and Healey 1990). When the fitness benefits of a high ration are greater for one sex than the other, that sex may be more willing to risk predation to obtain food (Abrahams and Dill 1989; Holtby and Healey 1990). The higher growth rate of female plaice suggests that the fitness benefits of growth are greater for female plaice than for male plaice, perhaps because increases in fertility with body size are greater for females than for males. If so, females would be expected to risk a higher foraging rate than males and consequently obtain a higher food ration. Because the optimal temperature for growth increases with ration size (e.g., Brett et al. 1969; Elliott 1975; Woiwode and Adelman 1991), females would be expected to occupy warmer temperatures than males. Similarly, as plaice abundance increases and per capita food availability declines, females may be willing to risk increasing their foraging rate to maintain a relatively high ration but males may not, so that food ration declines for males as does their optimal temperature for growth, resulting in a shift in male distribution toward colder temperatures and an increase in the difference in temperature distribution between males and females.

A key component of this conceptual model is a higher foraging rate in females than in males. Differences between male and female plaice in geographic distribution and bathymetric pattern are consistent with this assumption. For both these aspects of distribution, females tend to be more spread out than males (Swain and Morin 1996, 1997), even though females tend to be less abundant than males for ages up to about 9 year (R. Morin, unpublished data). This is consistent with a higher level of competitive interaction among females than among males due to higher foraging rates in females.

Variation in cod abundance was the factor most closely associated with variation in the median temperature occupied by both male and female plaice, with both sexes occupying warmer water as cod abundance increased. This result is opposite to that predicted on the basis of declining food rations for plaice due to increased interspecific competition at high levels of cod abundance. As cod abundance increases in the southern Gulf, peak cod densities shift from warm shallow waters to the cold waters and intermediate depths preferred by plaice (Swain 1993; Swain and Kramer 1995; Swain and Morin 1997). The coincident shift of plaice distribution into warmer water may reflect a response to changes in relative habitat suitability associated with this shift in cod distribution.

Unlike median temperature, the average temperature occupied by plaice was unrelated to cod abundance. This contrast between results for the median and the average suggests that the effect of cod abundance may involve shifts in plaice temperature distribution near its center as opposed to its limits. However, effects of cod abundance on the difference in temperature distribution between the sexes were not consistent with these within-sex results. Cod abundance had a significant effect on the difference in average temperature occupied but not on the difference in median temperature. Variation in the difference in median temperature may be dominated by the effect of plaice abundance because this effect differed strongly between the sexes (significant for males but not for females) whereas the effect of cod abundance did not (significant for both sexes). The effect on the difference between the sexes in average temperature occupied is consistent with a stronger response by males than females to variation in cod abundance. This might occur because of the closer association of males with the cold water into which cod distribution shifts at high abundance.

The model that I propose here to explain the sex-specific temperature distributions of plaice in the southern Gulf leads to a number of testable predictions. First, females should have a higher rate of natural mortality than males because of the trade-off between foraging rate and risk of predation. Second, as the difference in temperature distribution between the sexes increases, so should the differences in rates of growth and natural mortality. However, spatial interactions with cod may blur these predictions. For example, if male plaice respond more strongly than females to shifts in cod distribution, showing a greater shift into warm water (i.e., away from the optimal temperature for growth given their foraging rate) with increases in cod abundance, then a decrease in the difference in temperature distribution between the sexes might not be associated with decreases in the differences in growth and natural mortality rates. Further work on cod–plaice interactions is required to achieve a better understanding of the interrelationships among sex-specific temperature distributions and rates of growth and mortality in plaice.

Acknowledgements

I thank D. McKay for help with data processing, R. Morin for helpful discussion of the work, and M.A. Rodriguez, R.I. Perry, R. Morin, J.A. Hutchings, E.M.P. Chadwick, and an anonymous reviewer for comments on the manuscript.

References

Abrahams, M.V., and Dill, L.M. 1989. A determination of the energetic equivalence of the risk of predation. Ecology, **70**: 999–1007.

Baker, C.D., Neill, W.H., Jr., and Strawn, K. 1970. Sexual difference in heat resistance of the Ozark minnow, *Dionda nubila* (Forbes). Trans. Am. Fish. Soc. **99**: 588–591.

Boltz, J.M., Siemien, M.J., and Stauffer, J.R., Jr. 1987. Influence of starvation on the preferred temperature of *Oreochromis mossambicus* (Peters). Arch. Hydrobiol. **110**: 143–146.

Brett, J.R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Am. Zool. **11**: 99–113.

Brett, J.R., Shelbourn, J.E., and Shoop, C.T. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Board Can. **26**: 2363–2394.

Crowder, L.B., and Magnuson, J.J. 1983. Cost-benefit analysis of temperature and food resource use: a synthesis with examples from the fishes. *In* Behavioral energetics: the cost of survival in vertebrates. *Edited by* W.P. Aspey and S.I. Lustick. Ohio University Press, Columbus. pp. 189–221.

Edgington, E.S. 1987. Randomization tests. 2 ed. Dekker, New York.

Elliott, J.M. 1975. The growth rate of brown trout (*Salmo trutta* L.) fed on reduced rations. J. Anim. Ecol. **44**: 823–842.

Elliott, J.M. 1979. Energetics of freshwater teleosts. *In* Fish phenology: anabolic adaptiveness in teleosts. *Edited by* P.J. Miller. Academic Press, London. pp. 29–61.

Fry, F.E.J. 1971. The effect of environmental factors on the physiology of fish. *In* Fish physiology. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, New York. pp. 1–98.

Fujio, Y., Nakajima, M., and Nagahama, Y. 1990. Detection of a low temperature-resistant gene in the guppy (*Poecilia reticulata*), with reference to sex-linked inheritance. Jpn. J. Genet. **65**: 201–207.

Gilbert, D., Pettigrew, B., Swain, D., and Couture, M. 1996. State of the Gulf of St. Lawrence: oceanographic conditions in 1994. Can. Data Rep. Hydrogr. Ocean Sci. No. 143.

Gilliam, J.F., and Fraser, D.F. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology, **68**: 1856–1862.

Hagen, D.W. 1964. Evidence of adaptation to environmental temperatures in three species of *Gambusia* (Poeciliidae). Southwest. Nat. **9**: 6–19.

Holtby, L.B., and Healey, M.C. 1990. Sex-specific life history tactics and risk-taking in coho salmon. Ecology, **71**: 678–690.

Hurlbut, T., and Clay, D. 1990. Protocols for research vessel cruises within the Gulf Region (demersal fish) (1970–1987). Can. Manuscr. Rep. Fish. Aquat. Sci. No. 2082.

Javaid, M.Y., and Anderson, J.M. 1967. Influence of starvation on selected temperature of some salmonids. J. Fish. Res. Board Can. **24**: 1515–1519.

Johansen, P.H., and Cross, J.A. 1980. Effects of sexual maturation and sex steroid hormone treatment on the temperature preference of the guppy, *Poecilia reticulata* (Peters). Can. J. Zool. **58**: 586–588.

Krebs, J.R., and Davies, N.B. 1981. An introduction to behavioural ecology. Sinauer, Sunderland, Mass.

Kwain, W., and McCauley, R.W. 1978. Effects of age and overhead illumination on temperatures preferred by underyearling rainbow trout, *Salmo gairdneri*, in a vertical temperature gradient. J. Fish. Res. Board Can. **35**: 1430–1433.

Mac, M.J. 1985. Effects of ration size on preferred temperature of lake charr *Salvelinus namaycush*. Environ. Biol. Fishes, **14**: 227–231.

Macpherson, E., and Duarte, C.M. 1991. Bathymetric trends in demersal fish size: is there a general relationship? Mar. Ecol. Prog. Ser. **71**: 103–112.

Magnuson, J.J., Crowder, L.B., and Medvick, P.A. 1979. Temperature as an ecological resource. Am. Zool. **19**: 331–343.

Mahon, R., Smith, R.W., Bernstein, B.B., and Scott, J.S. 1984. Spatial and temporal patterns of groundfish distributions on the Scotian Shelf and in the Bay of Fundy, 1970–1981. Can. Tech. Rep. Fish. Aquat. Sci. No. 1300.

McCauley, R.W., and Huggins, N.W. 1979. Ontogenetic and nonthermal seasonal effects on thermal preferenda of fish. Am. Zool. **19**: 267–271.

McCauley, R.W., and Read, L.A.A. 1973. Temperature selection by juvenile and adult yellow perch (*Perca flavescens*) acclimated to 24 C. J. Fish. Res. Board Can. **30**: 1253–1255.

Milinski, M., and Heller, R. 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). Nature (Lond.), **275**: 642–644.

Morgan, M.J. 1993. Ration level and temperature preference of American plaice. Mar. Behav. Physiol. **24**: 117–122.

Morin, R., and Sinclair, A. 1993. Status of American plaice in NAFO Division 4T. DFO Atl. Fish. Res. Doc. No. 93/64. Department of Fisheries and Oceans, Stock Assessment Secretariat, Ottawa, Ont.

Nakken, O., and Raknes, A. 1987. The distribution and growth of Northeast Arctic cod in relation to bottom temperatures in the Barents Sea, 1978–1984. Fish. Res. **5**: 243–252.

Otto, R.G., Kitchell, M.A., and Rice, J.O. 1976. Lethal and preferred temperatures of the alewife (*Alosa pseudoharengus*) in Lake Michigan. Trans. Am. Fish. Soc. **104**: 96–106.

Perry, R.I., and Smith, S.J. 1994. Identifying habitat associations of marine fishes using survey data: an application to the northwest Atlantic. Can. J. Fish. Aquat. Sci. **51**: 589–602.

Powles, P.M. 1965. Life history and ecology of American plaice (*Hippoglossoides platessoides* F.) in the Magdalen Shallows. J. Fish. Res. Board Can. **22**: 565–598.

Reynolds, W.W., and Casterlin, M.E. 1978. Ontogenetic change in preferred temperature and diel activity of the yellow bullhead, *Ictalurus natalis*. Comp. Biochem. Physiol. A Comp. Physiol. **59**: 409–411.

Reynolds, W.W., and Casterlin, M.E. 1979*a*. Behavioral thermoregulation and the 'final preferendum' paradigm. Am. Zool. **19**: 211–224.

Reynolds, W.W., and Casterlin, M.E. 1979*b*. Role of temperature in the environmental physiology of fishes. *In* Environmental physiology of fishes. *Edited by* M.A. Ali. Plenum Press, New York. pp. 497–518.

Reynolds, W.W., McCauley, R.W., Casterlin, M.E., and Crawshaw, L.I. 1976. Body temperatures of behaviorally thermoregulating largemouth blackbass (*Micropterus salmoides*). Comp. Biochem. Physiol. A Comp. Physiol. **54**: 461–463.

Rose, G.A., and Leggett, W.C. 1988. Atmosphere–ocean coupling and Atlantic cod migrations: effects of wind-forced variations in sea temperatures and currents on nearshore distributions and catch rates of *Gadus morhua*. Can. J. Fish. Aquat. Sci. **45**: 1234–1243.

Rose, G.A., and Leggett, W.C. 1989. Interactive effects of geophysically-forced sea temperatures and prey abundance on mesoscale coastal distributions of a marine predator, Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **46**: 1904–1913.

SAS Institute Inc. 1990. SAS/STAT user's guide, version 6, edition 4. SAS Institute Inc., Cary, N.C.

Scott, J.S. 1982. Depth, temperature and salinity preferences of common fishes of the Scotian Shelf. J. Northwest Atl. Fish. Sci. **3**: 29–39.

Sih, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. Ecology, **63**: 786–796.

Sinclair, A. 1992. Fish distribution and partial recruitment: the case of eastern Scotian Shelf cod. J. Northwest Atl. Fish. Sci. **13**: 15–24.

Sinclair, A., Chouinard, G., Swain, D., Nielsen, G., Hanson, M., Currie, L., Hurlbut, T., and Hébert, R. 1995. Assessment of the southern Gulf of St. Lawrence cod stock, March 1995. DFO Atl. Fish. Res. Doc. No. 95/39. Department of Fisheries and Oceans, Stock Assessment Secretariat, Ottawa, Ont.

Stott, W., Ferguson, M.M., and Tallman, R.F. 1992. Genetic population structure of American plaice (*Hippoglossoides platessoides*) from the Gulf of St. Lawrence, Canada. Can. J. Fish. Aquat. Sci. **49**: 2538–2545.

Stuntz, W.E., and Magnuson, J.J. 1976. Daily ration, temperature selection, and activity of bluegill. *In* Thermal ecology II. *Edited by* G.W. Esch and R.W. McFarlane. ERDA Symp. Ser., CONF-750425. Technical Information Service, Springfield, Va. pp. 180–184.

Swain, D.P. 1993. Age- and density-dependent bathymetric pattern of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **50**: 1255–1264.

Swain, D.P., and Kramer, D.L. 1995. Annual variation in temperature selection by Atlantic cod *Gadus morhua* in the southern Gulf of St. Lawrence, Canada, and its relation to population size. Mar. Ecol. Prog. Ser. **116**: 11–23.

Swain, D.P., and Morin, R. 1996. Relationships between geographic distribution and abundance of American plaice (*Hippoglossoides platessoides*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **53**: 106–119.

Swain, D.P., and Morin, R. 1997. Effects of age, sex and abundance on the bathymetric pattern of American plaice (*Hippoglossoides platessoides*) in the southern Gulf of St. Lawrence. J. Fish Biol. **50**: 181–200.

Swain, D.P., and Wade, E.J. 1993. Density-dependent geographic distribution of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **50**: 715–733.

Tremblay, M.J., and Sinclair, M. 1985. Gulf of St. Lawrence cod: age-specific geographic distributions and environmental occurrences from 1971 to 1981. Can. Tech. Rep. Fish. Aquat. Sci. No. 1387.

Walsh, S.J. 1982. Distribution and abundance of pre-recruit and commercial-sized American plaice on the Grand Bank. J. Northwest Atl. Fish. Sci. **3**: 149–157.

Wildhaber, M.L., and Crowder, L.B. 1990. Testing a bioenergetics-based habitat choice model: bluegill (*Lepomis macrochirus*) responses to food availability and temperature. Can. J. Fish. Aquat. Sci. **47**: 1664–1671.

Woiwode, J.G., and Adelman, I.R. 1991. Effects of temperature, photoperiod, and ration size on growth of hybrid striped bass × white bass. Trans. Am. Fish. Soc. **120**: 217–229.

Changes in the planktonic food web of a new experimental reservoir[1]

M.J. Paterson, D. Findlay, K. Beaty, W. Findlay, E.U. Schindler, M. Stainton, and G. McCullough

Abstract: Changes in plankton community structure were examined in an experimental reservoir (Lake 979) before and after impoundment. The role of allochthonous organic matter in planktonic food webs is unclear, and reservoir creation can be viewed as an extreme manipulation of terrestrial organic matter inputs. After impoundment of Lake 979, concentrations of phosphorus, nitrogen, and dissolved organic carbon increased as a result of decomposition of flooded terrestrial organic matter. In the first year of impoundment, mean bacterial biomass increased 10×, and individual bacterial cell volumes increased 2× over pre-flooding averages. Phytoplankton production and biomass decreased to approximately 25% of pre-flooding levels. Zooplankton biomass and production by Cladocera increased 10×, and zooplankton community composition changed from dominance by small-sized *Bosmina longirostris* to dominance by large *Daphnia rosea*. In the first year of impoundment, production by Cladocera usually exceeded phytoplankton ^{14}C productivity, suggesting that the main pathway of carbon flow to secondary producers shifted from an autochthonous to an allochthonous base derived from flooded terrestrial vegetation. In the second year of flooding, bacterial biomass decreased and phytoplankton biomass was higher than in the two previous years of study.

Résumé : Des changements touchant la structure de la communauté planctonique ont été examinés dans un réservoir expérimental (lac 979) avant et après mise en eau. Le rôle de la matière organique allochtone dans les réseaux trophiques planctoniques est obscur et la création de réservoirs peut être vue comme une manipulation extrême des apports en matière organique terrestre. Après la mise en eau du lac 979, les concentrations de phosphore, d'azote et de carbone organique dissous ont augmenté par suite de la décomposition de la matière organique terrestre inondée. Au cours de la première année de la mise en eau, la biomasse bactérienne moyenne a décuplé et le volume des cellules bactériennes individuelles a doublé par rapport aux moyennes d'avant mise en eau. La production et la biomasse de phytoplancton ont diminué à environ 25 % des niveaux d'avant inondation. La production et la biomasse de zooplancton et la production de cladocères ont décuplé et la composition de la communauté de zooplancton a changé : alors qu'avant elle était dominée par des *Bosmina longirostris* de petite taille, elle est devenue dominée par *Daphnia rosea* de grande taille. Au cours de la première année de la mise en eau, la production de cladocères a habituellement dépassé la productivité en ^{14}C du phytoplancton, ce qui indiquerait que la principale voie du flux du carbone vers les producteurs secondaires est passé d'une base autochtone à une base allochtone provenant de la végétation terrestre inondée. Au cours de la deuxième année suivant la création du réservoir, la biomasse bactérienne a diminué et la biomasse phytoplanctonique était plus élevée qu'au cours des deux années d'étude précédentes.
[Traduit par la Rédaction]

Introduction

The creation of new reservoirs frequently results in short-term increases in production by fish and invertebrates (Ostrofsky 1978; Baxter and Glaude 1980). Typically, it is assumed that increases in secondary productivity are supported by greater phytoplankton production stimulated by the release of nutrients from decomposing organic matter (Ostrofsky 1978). Although several studies have found higher planktonic primary production or phytoplankton biomass after the creation of reservoirs (e.g., Roche 1964; Duthie and Ostrofsky 1975), it is unclear whether this is sufficient to support observed increases in secondary production (Adam et al. 1983). The addition of large amounts of newly flooded terrestrial organic matter may also stimulate bacterial activity and increase carbon flow to higher trophic levels through the detrital pathway. For example, Romanenko (1979) found that plankton respiration exceeded primary production by nearly two times in a newly formed reservoir on the Volga River.

There is considerable debate about the influence of allochthonous detrital matter and bacterial production on phytoplankton and zooplankton communities (e.g., Jones 1992; Tranvik 1992). It is uncertain to what extent bacteria may support zooplankton production or how changes in the relative availability of bacteria and phytoplankton may influence zooplankton species composition. Several laboratory studies indicate that bacteria may compete with phytoplankton for essential nutrients such as phosphorus (Rhee 1972; Currie and Kalff 1984; Vadstein and Olsen 1989), but evidence of competition between bacteria and phytoplankton in natural systems is equivocal (Berman 1985; Currie 1990; Jones 1992). New reservoirs provide an excellent opportunity to study the effects of large inputs of allochthonous organic matter on the planktonic food web.

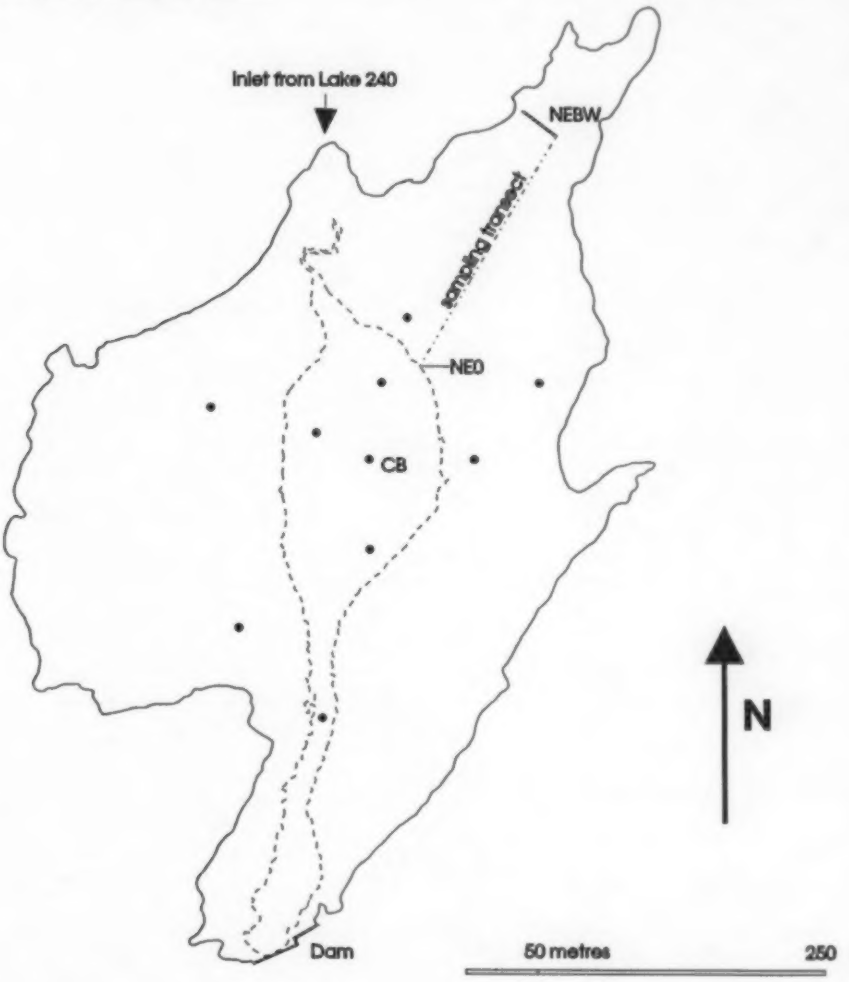
This study examines the short-term effects of impoundment

Received April 11, 1996. Accepted October 7, 1996.
J13402

M.J. Paterson, D. Findlay, K. Beaty, W. Findlay, E.U. Schindler, M. Stainton, and G. McCullough. Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada.

[1] Contribution No. 22 of the Experimental Lakes Area Reservoir Project (ELARP).

Fig. 1. Station locations (●) on Lake 979. Some stations over the flooded peat were moved slightly in 1994 because of interference from floating peat islands. The pre-impoundment shoreline (until June 1993) is indicated with a broken line. NEBW, northeast boardwalk; CB, centre buoy; NE0, beginning of sampling transect.



on the planktonic food web in Lake 979, a small experimental reservoir in the Experimental Lakes Area (ELA), northwestern Ontario. We document shifts in plankton community structure that occurred after flooding and discuss mechanisms underlying observed changes. In particular, we consider the effects of alterations in hydrology, nutrient availability, zooplankton grazing, and competition between bacteria and phytoplankton.

Site description

Lake 979 (49°38′N, 93°43′W) is surrounded by peatland and is immediately downstream of Lake 240 (Fig. 1). Lake 240 has a 723 ha catchment that includes five other lakes. A dam was constructed at the outflow of Lake 979, and between June 28 and July 5, 1993, the water level was raised 1.3 m. This increased the maximum depth from 1.2 to 2.5 m, the lake area from 2.4 to 16 ha, and led to a 7.4× increase in lake volume. On October 5, 1993, the water level was drawn down 1 m to mimic the water regimes of many northern hydroelectric reservoirs, which experience similar drawdowns in response to increased power demands in winter. In 1994, flooding was reinitiated on May 26, and the reservoir was filled by June 27. Drawdown began on September 29. Fish inhabiting Lake 979 both before and after flooding included northern pike (*Esox lucius*), yellow perch (*Perca flavescens*), white sucker (*Catastomus commersoni*), and finescale dace (*Chrosomus neogaeus*).

Methods

Hydrology and water chemistry

Inflows from Lake 240 into Lake 979 were measured with a calibrated concrete 120° V-notch recording weir. Water levels during the ice-free season were monitored by a data logger in a stilling well. Samples for water chemistry were collected every 2 weeks at the centre buoy (Fig. 1) and were analyzed according to Stainton et al. (1977). During impoundment, water chemistry was also monitored monthly at the northeast arm boardwalk, in approximately 0.3 m of water over flooded peat (Fig. 1). Chemical variables deemed potentially important to bacteria, phytoplankton, and zooplankton included total dissolved phosphorus (TDP), suspended phosphorus, dissolved organic carbon (DOC), suspended carbon, nitrate (NO_3-N), ammonium (NH_4-N), total dissolved nitrogen (TDN), suspended nitrogen, oxygen, and pH.

Dissolved nutrients such as TDP, TDN, and DOC were operationally defined as those passing through a GF/C filter with a nominal pore size of 1.2 μm. As a result, many bacteria passed through the filter (D. Findlay, unpublished data) and the "dissolved" fraction includes nutrients associated with both bacteria and dissolved organic matter (DOM). Both dissolved and suspended nutrients were measured directly, and total nutrient concentrations were determined from the sum of the two fractions.

Phytoplankton and bacteria

Water samples were collected at 2- to 4-week intervals at the centre buoy using an integrating sampler (Shearer 1978). Samples were then subsampled for counts of phytoplankton and bacteria and for estimation of ^{14}C phytoplankton photosynthesis.

For phytoplankton enumeration, 10-mL aliquots of samples preserved in Lugol's solution were allowed to settle for 24 h. Phytoplankton were counted with an inverted microscope using the Utermohl technique (Nauwerck 1963). Cell sizes were determined from averages calculated from up to 50 individuals of each species (actual counts depended on relative abundance of each species in a sample). Counts were converted to wet weights by applying the geometric formula that best fit each cell shape and assuming a specific gravity of 1.

For bacteria, 1- to 2-mL aliquots were filtered onto a prestained polycarbonate filter (pore size 0.2 μm) and stained using the DAPI technique (Porter and Feig 1980). Bacteria were enumerated and measured under an epifluorescent microscope equipped with a mercury lamp. Twenty-four random fields were examined from each sample. Bacteria were enumerated at 1-month intervals.

Phytoplankton production was estimated using the ^{14}C technique of Fee et al. (1992). Algal turnover was estimated using (*i*) P^{B}_{m}, the rate of ^{14}C production per unit of chlorophyll at optimal irradiance, and (*ii*) $P_{opt}{\cdot}B^{-1}$, the rate of ^{14}C production per unit of phytoplankton biomass at optimal irradiance. Both measures are presented below because trends for each were slightly different. We have chosen to use P^{B}_{m} and $P_{opt}{\cdot}B^{-1}$ rather than P/B (^{14}C production/phytoplankton biomass) because we wished to remove the influence of changes in light on algal growth rates. Changes in P/B were generally similar to changes in $P_{opt}{\cdot}B^{-1}$ (D. Findlay and E.U. Schindler, unpublished data).

Zooplankton

Beginning in June 1992, zooplankton were sampled weekly at five randomly located stations in Lake 979 (Fig. 1). After flooding, an additional five stations were established over the newly flooded peat in Lake 979 in water at least 0.5 m deep. Zooplankton were sampled during the day using a 7 cm diameter wire-reinforced plastic tube that collected an integrated sample from the entire water column. All samples were sieved through a 53-μm net, narcotized with methanol (Gannon and Gannon 1975), and preserved with sugar–formalin to a final concentration of approximately 3% formalin. For all dates, a minimum total of 300 crustacean zooplankton were counted and identified to species for each of the inshore and offshore regions. Zooplankton were measured in separate counts using a computerized caliper system (Allen et al. 1994), and lengths were converted to biomasses using regression equations in Malley et al. (1989) and McCauley (1984). Preservation in formalin does not strongly affect length determinations for common zooplankton at ELA (Malley et al. 1989). In this study, a minimum of 100 animals of each common species was measured for each sampling date, whenever possible.

Productivity of Cladocera was estimated using the technique of Saunders and Lewis (1988). This approach assumes continuous recruitment and estimates productivity as the product of average population biomass (*B*) and the population growth rate (*g*) in a sampling interval. As in previous studies, the population birth rate (*b*) was used to estimate *g*. Our productivity estimates should be regarded with caution because they use a measure of numerical growth rate, *b*, to estimate biomass growth rate (Anderson and Benke 1994). Eggs were counted in at least 100 individuals of each common species (whenever possible) and were converted to birth rates using the formula of Paloheimo (1974). Temperature-dependent egg development rates for each species were determined from the literature. Lake 979 did not strongly thermally stratify at any time. Loose eggs were counted and attributed to common species based on their relative abundance. Carbon content of Cladocera was assumed to be 45% of dry weight (Andersen and Hessen 1991).

The spatial distribution of plankton and sampling precision

On several occasions, water chemistry, phytoplankton, bacteria, and zooplankton biomass were measured along a transect extending from the centre buoy to shore (Fig. 1). Concentrations of most parameters increased from the centre of the pond toward shore, both before and after flooding (see below). As a result, among-station standard errors of mean estimates (SEM) for most parameters are higher than those encountered in more uniformly mixed systems (e.g., Downing et al. 1987). For example, SEMs for zooplankton were occasionally as high as 40%. Estimates of within-station variance for zooplankton were undertaken on six different occasions and were always low (<20% for three replicates). Within-station variability for water chemistry, bacteria, and phytoplankton in other lakes at ELA is similarly low.

Results

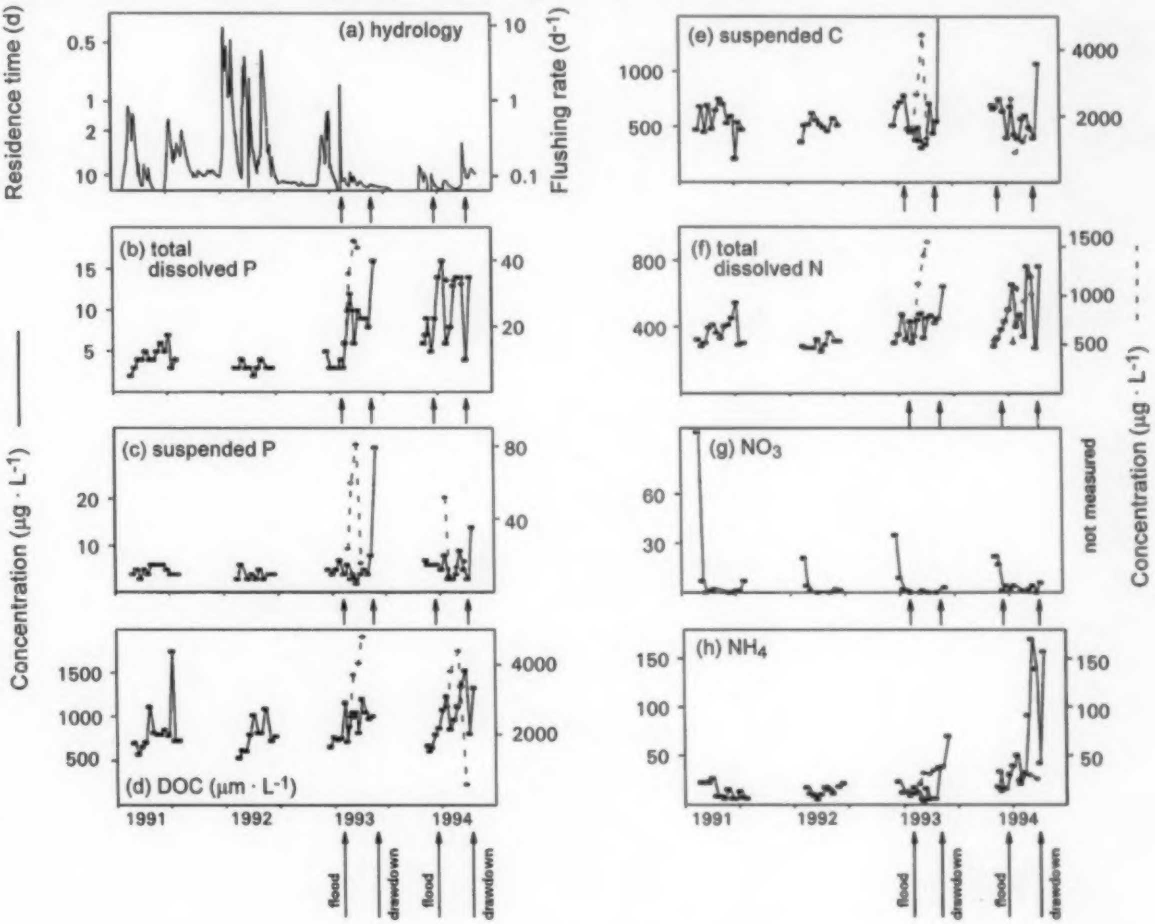
Hydrology, nutrients, and water chemistry

Prior to impoundment, flushing rates in Lake 979 were highly variable, with theoretical residence times as short as 0.3–0.5 days (Fig. 2*a*). Flooding increased the pond volume by 7.4×, which substantially increased residence times. During impoundment, residence times were usually >10 days. True exchange times at the centre of the pond were less than these theoretical values because the reservoir did not completely mix (see below).

Average concentrations of TDP at the centre buoy increased from 7.3 $\mu g{\cdot}L^{-1}$ before flooding to 12.2 and 15.7 $\mu g{\cdot}L^{-1}$ after flooding in 1993 and 1994, respectively (Fig. 2*b*). In 1993, centre-buoy concentrations of other nutrients were not strongly affected by impoundment except during drawdown. Concentrations of P, N, and C increased between 2 and 4× above summer averages after drawdown in October 1993 (Figs. 2*b*–2*h*). Concentrations of DOC and TDN increased at the centre buoy in 1994, 1 year after flooding. Elevated concentrations of NH_4-N occurred in the fall of both 1993 and 1994.

Concentrations of most nutrients at the northeast boardwalk (over flooded peat) were 2–10× higher than in the open pond (Figs. 2*b*–2*h*). Samples collected at the northeast boardwalk and centre buoy represented extreme ends of a chemical gradient extending from shore to the open pond (e.g., Fig. 3). In the inshore regions, nutrients were leached into shallow, quiescent water that was protected by flooded trees and mixed slowly with the open pond. At the centre buoy, nutrients generated from decomposing peat were diluted with water from upstream Lake 240 and concentrations of most nutrients were strongly correlated with changes in water residence times both

Fig. 2. Changes in (*a*) hydrologic residence times and (*b*–*h*) concentrations of dissolved and suspended concentrations of P, C, N, NO_3-N, and NH_4-N in the open pond (centre buoy) and over the flooded peat (NEBW), 1991–1994. Centre-buoy concentrations (——) are depicted on the left-hand scale of each graph, whereas concentrations at the northeast boardwalk (- - -) are depicted on the right-hand scale. NO_3 was not measured at the northeast boardwalk. Flushing rate = (daily inflow from Lake 240)/(lake volume).



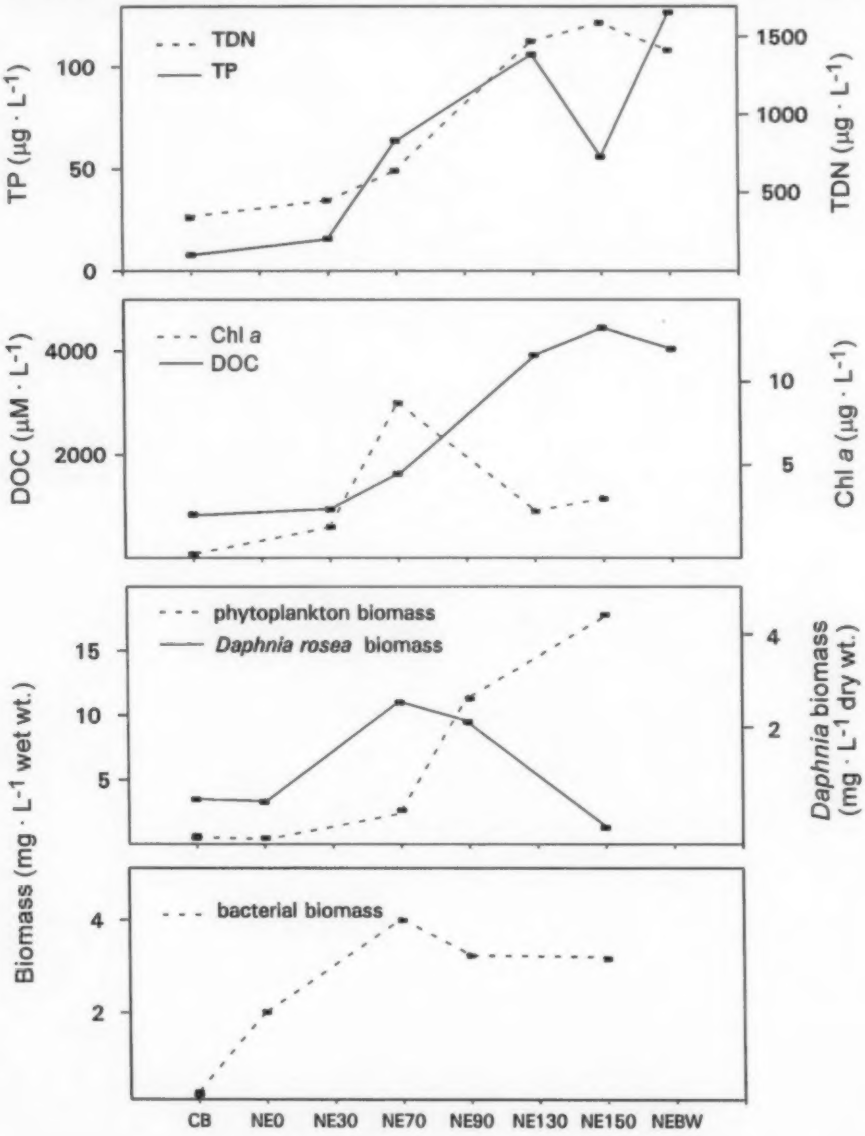
before and after flooding (Table 1). Nutrient concentrations declined during periods of high inflow and approached values in oligotrophic Lake 240. There were no large changes in the concentrations of nutrients in water inflows from Lake 240 over the 4-year period of study. For example, concentrations of TDP never exceeded 3 $\mu g \cdot L^{-1}$. Nutrient concentrations increased in the pond when longer residence times prevailed in Lake 979 because of the influence of the surrounding wetland and in-pond decomposition processes. Large increases in concentrations of P and other nutrients observed during drawdown reflected the movement into the pond of inshore water and pore water "squeezed" from the peat.

Impoundment also affected oxygen concentrations and pH in Lake 979. Oxygen was not measured in 1991 and 1992, but the pond was well mixed and concentrations were probably always near saturation. After flooding, oxygen concentrations were frequently low at the pond surface (approximately 50% saturation) and often approached zero over the newly flooded peat and near the pond bottom (J. Rudd, Freshwater Institute, Winnipeg, Man., personal communication). Surface samples usually contained at least 2–3 $mg \cdot L^{-1}$. The mean pH of Lake 979 declined from 6.7 to 6.2 after flooding. Impoundment did not result in large sustained changes in average temperature, light extinction (E.U. Schindler, unpublished data), or suspended C at the centre buoy.

Phytoplankton

Phytoplankton biomass and chlorophyll *a* were consistently low at the centre buoy in 1991 and 1992 (Fig. 4*a*). Prior to flooding in 1993, abundance of phytoplankton increased approximately 2× during a period of low hydrologic flushing. Impoundment in June led to a 70% decline in phytoplankton biomass from the pre-flooding average of 0.45 to 0.13 $mg \cdot L^{-1}$. Epilimnetic phytoplankton biomass in upstream Lake 240 was 0.4 $mg \cdot L^{-1}$ at this time. The decrease in phytoplankton in Lake 979 was not simply a consequence of dilution caused by deepening of the water column. Average algal biomass per square metre of pond surface at the centre buoy also declined

Fig. 3. Changes in several limnological variables along a gradient extending from the centre of Lake 979 (CB) toward shore, August 10, 1993. Numbers on the *X*-axis indicate distance from the northeast shoreline of the original pond (NE0). Other abbreviations are as in Fig. 1.



from a pre-flooding average (1992 and early 1993) of 0.54 to 0.39 g·m^{-2} in July–September 1993. Low algal biomasses persisted until October 1993, when phytoplankton increased with drawdown. Phytoplankton biomass was again high in the spring of 1994 and declined immediately following impoundment in June. There was a transient increase in biomass in July that was associated with a period of low flushing and elevated P concentrations. Average phytoplankton biomass and chlorophyll *a* levels were higher in 1994 than in all previous years. Phytoplankton biomass was highest in the most inshore regions of the pond (e.g., Fig. 3).

Throughout the study, the phytoplankton community of Lake 979 was predominantly composed of small (<30 µm) cryptophytes, chrysophytes, and chlorophytes that could be consumed by zooplankton (Fig. 4*b*). Species composition changed somewhat after flooding (D. Findlay, unpublished data), but large changes in the proportion of edible algae were not observed.

Regular estimation of phytoplankton photosynthesis began in the spring of 1993 and consequently, only 4 weeks of pre-flooding data are available (Fig. 5*a*). In general, phytoplankton photosynthesis was correlated with changes in algal biomass. In 1993, flooding of Lake 979 resulted in a brief increase and subsequent decrease in photosynthesis (Fig. 5*a*), $P_{\mathrm{m}}^{\mathrm{B}}$, and $P_{\mathrm{opt}} \cdot B^{-1}$ (Fig. 5*c*). In 1994, refilling of the reservoir was followed by an initial decline of phytoplankton photosynthesis.

Table 1. Correlations between various limnological variables measured at the centre buoy and water residence time.

	Before flooding	After flooding
Total P	0.85***	0.52*
Dissolved P	0.79***	0.57*
Suspended P	0.55**	0.24
Dissolved N	0.75***	0.68**
Ammonium	–0.25	0.43
Nitrate	–0.57**	0.01
DOC	0.52**	0.60**
Phytoplankton biomass	–0.10	0.25
Chlorophyll *a*	–0.11	0.50
Zooplankton biomass	0.72***	0.19

Note: Water residence times were calculated as one half the sum of the number of days of discharge required to fill two lake volumes (Canfield et al. 1984). Data collected immediately after drawdown were excluded. All values were $\log_{10}$ transformed before analysis. Probabilities were not corrected for multiple comparisons. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

In contrast to 1993, photosynthetic production subsequently increased, reaching a maximum in late August. and P^{B}_{m} and $P_{opt}{\cdot}B^{-1}$ were highest in August–September 1994.

Bacteria

Flooding of Lake 979 in June 1993 led to a large increase in bacterial biomass at the centre buoy (Fig. 6*a*) and changes in the relative abundance of phytoplankton and bacteria. Prior to flooding, average bacterial biomass was 27% of average phytoplankton biomass, but after flooding in 1993, average bacterial biomass exceeded phytoplankton biomass by approximately 9×. In 1994, bacterial biomass declined from 1993 post-flooding values, but still exceeded pre-flooding estimates by nearly 4×. At this time, average bacterial biomass was 70% of phytoplankton biomass. Bacterial biomass was also higher over the flooded peat than in the open pond (Fig. 3).

Impoundment of Lake 979 also affected bacterial size structure and morphology (Figs. 6*b* and 6*c*). Flooding led to an increase in mean individual biovolume from approximately 0.1 to 0.3 μm^3. In 1992 and 1993, the bacterial assemblage was dominated by coccoidal forms. In 1994, there was a sharp increase in the relative abundance of rod-shaped bacteria.

Zooplankton

Zooplankton biomass increased dramatically after impoundment (Fig. 7*a*). Biomass usually exceeded pre-flooding values by at least 10× and was greatest over the flooded peat. Changes in zooplankton biomass were associated with large shifts in species composition (Fig. 7*b*). Prior to flooding, Lake 979 was dominated by *Bosmina longirostris*, *Polyphemus pediculus*, and cyclopoid copepods (*Diacyclops bicuspidatus thomasi*, *Tropocyclops prasinus mexicanus*, *Mesocyclops edax*). *Daphnia galeata mendotae* and *D. rosea* occurred only in low abundance. With impoundment, species common to Lake 240 briefly invaded (*D. bicuspidatus thomasi*, *Holopedium gibberum*, *D. galeata mendotae*). Within 2 weeks, numbers of *D. rosea* increased, and this species dominated zooplankton biomass thereafter (except for a brief period in the spring of 1994, prior to flooding). After impoundment, numbers of *Chaoborus* spp., an invertebrate predator, also increased dramatically (Fig. 8). *Chaoborus* densities depicted in Fig. 8 are probably underestimates, because all samples were collected during the day. Many *Chaoborus* species migrate vertically and live in the sediments at this time.

The two most abundant species of zooplankton were *B. longirostris* and *D. rosea* (Fig. 9). In 1992, *B. longirostris* densities, egg ratios, and birth rates were low throughout most of the year (Figs. 9*a*–9*c*). Prior to impoundment, numbers of *D. rosea* were so low that few measures of lengths and egg ratios were possible (Figs. 9*e*–9*h*). In spring 1993, increases in densities of *B. longirostris* were initially associated with high birth rates and high phytoplankton densities. Egg ratios declined as numbers of *B. longirostris* increased while average size (Fig. 9*d*) and size at first reproduction (M. Paterson, unpublished data) remained unchanged. This suggests the onset of density-dependent food limitation (e.g., Gliwicz and Boavida 1996). Immediately after impoundment in June, densities of both *B. longirostris* and *D. rosea* were low, and egg ratios and birth rates increased sharply. As numbers of both species increased, egg ratios declined, and severe food limitation was evident by midsummer. In September, densities of both species decreased, and egg ratios increased. These changes were associated with the onset of sexual reproduction and increasing densities of *Chaoborus* (Fig. 8). In 1994, densities of *D. rosea* increased sharply in the spring during a period of high birth rates. Between June and September, *D. rosea* egg ratios and densities were relatively constant. *Bosmina longirostris* densities were exceptionally low in 1994, and few measures of lengths and egg ratios were possible. Mean lengths of *B. longirostris* were not strongly affected by impoundment, whereas *D. rosea* sizes increased from 1992 to 1994 (Figs. 9*d* and 9*h*).

Flooding of Lake 979 resulted in a large increase in productivity by Cladocera (Fig. 5*b*). In 1993, post-flooding productivity in the open pond often equalled or exceeded phytoplankton photosynthesis. In 1994, cladoceran productivity was similar to 1993 but never exceeded phytoplankton ^{14}C productivity. Cladocera made up greater than 80% of the biomass of crustacean zooplankton on all dates except September 1992 and May of all years.

Discussion

Prior to impoundment, nutrient concentrations and biomasses of bacteria, phytoplankton, and zooplankton in Lake 979 were similar to other unmanipulated lakes at ELA (Armstrong and Schindler 1971; Salki 1995; Findlay et al. 1994, 1996). Nutrients, bacteria, phytoplankton, and zooplankton did not change dramatically between 1991 and 1994 in unmanipulated lakes at ELA (Salki 1995; Findlay et al. 1996; M. Stainton, D. Findlay, and M. Paterson, unpublished data). For example, mean annual epilimnetic phytoplankton biomass in lakes 239, 224, and 373 ranged from 0.30 to 0.40 $mg{\cdot}L^{-1}$ wet weight during this period (D. Findlay, unpublished data). Post-impoundment biomass of zooplankton in Lake 979 is among the highest recorded at ELA or elsewhere on the Canadian Shield (compare with Schindler and Novén 1971; Pace 1984; Yan 1986; Salki 1995). Biomasses of algae in Lake 979 observed in the first 6 weeks of flooding were the lowest ice-free epilimnetic values recorded at ELA, in a data set that covers 385 lake-years. These observations suggest it is unlikely that changes

Fig. 4. (*a*) Changes in phytoplankton biomass and chlorophyll *a* in Lake 979, 1991–1994. (*b*) Changes in phytoplankton size structure.

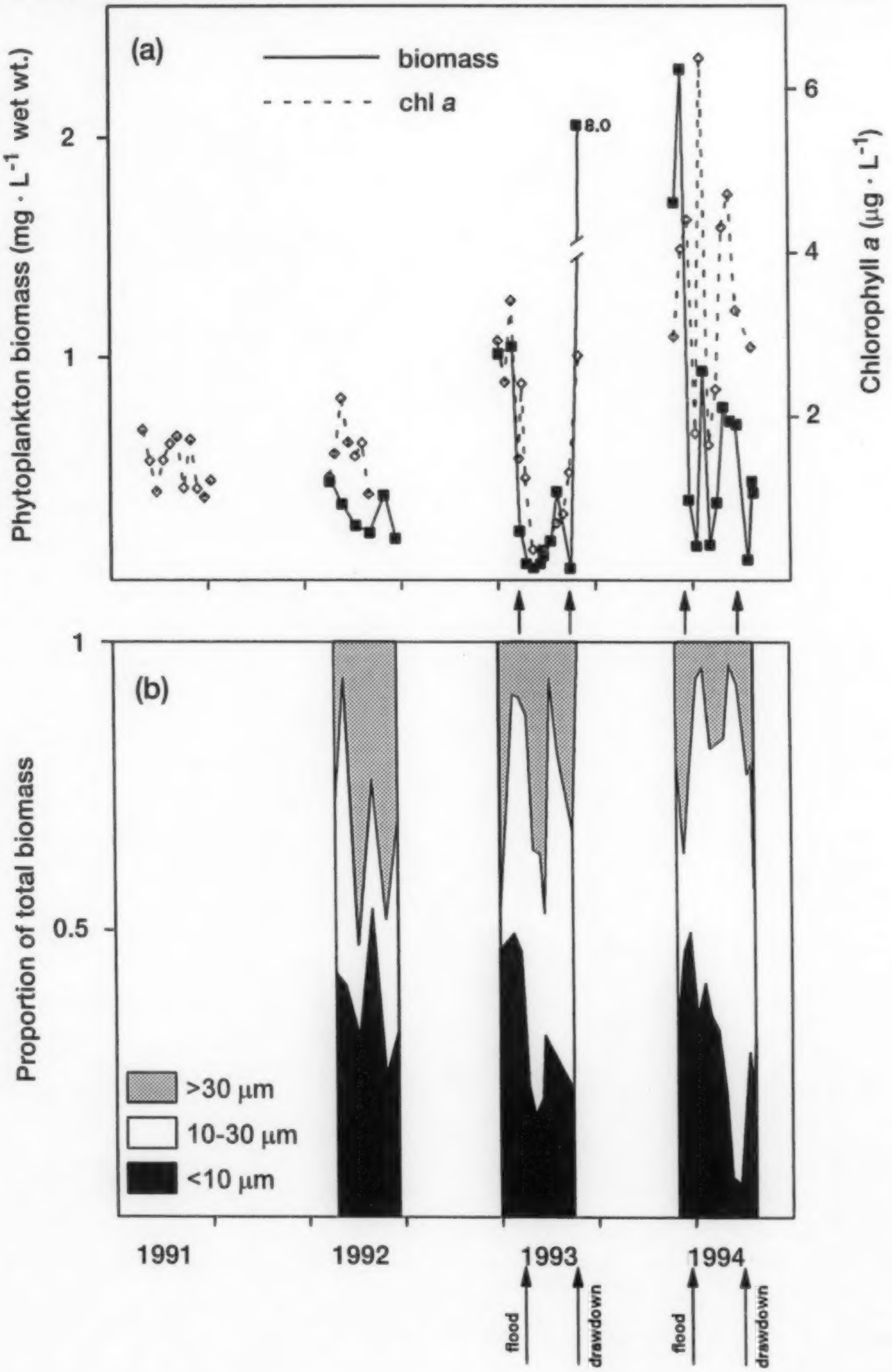


Fig. 5. (*a*) Changes in productivity by phytoplankton in Lake 979, 1993–1994. (*b*) Changes in productivity by Cladocera, 1992–1994. (*c*) Changes in phytoplankton P_m^B and $P_{opt} \cdot B^{-1}$.

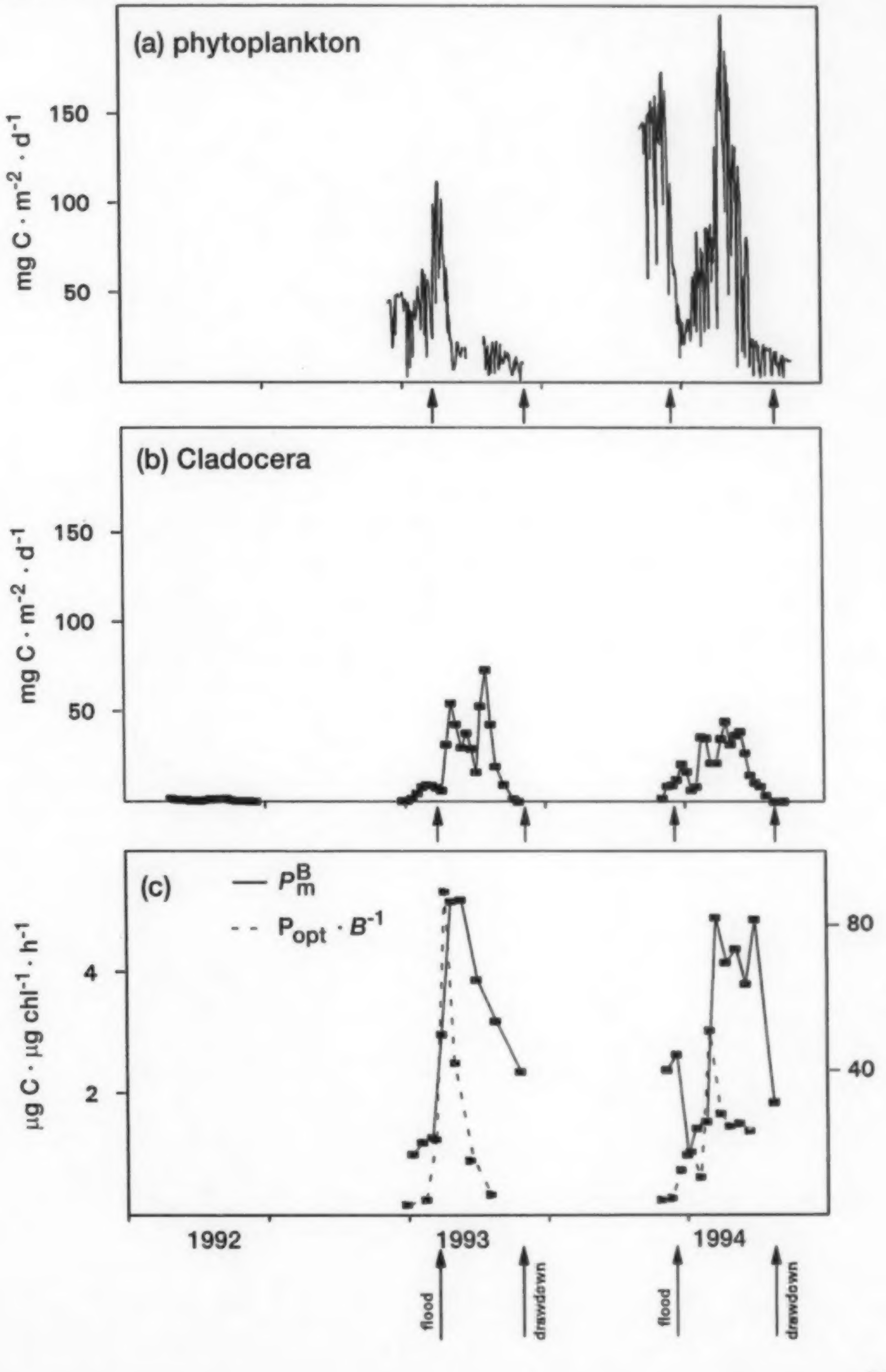


Fig. 6. (*a*) Changes in bacterial biomass at the centre buoy in Lake 979, 1992–1994. (*b*) Changes in mean cell volume of individual bacteria. Error bars are ± 1SD. (*c*) Changes in the numerical representation of rods and coccoids in the bacterial assemblage.

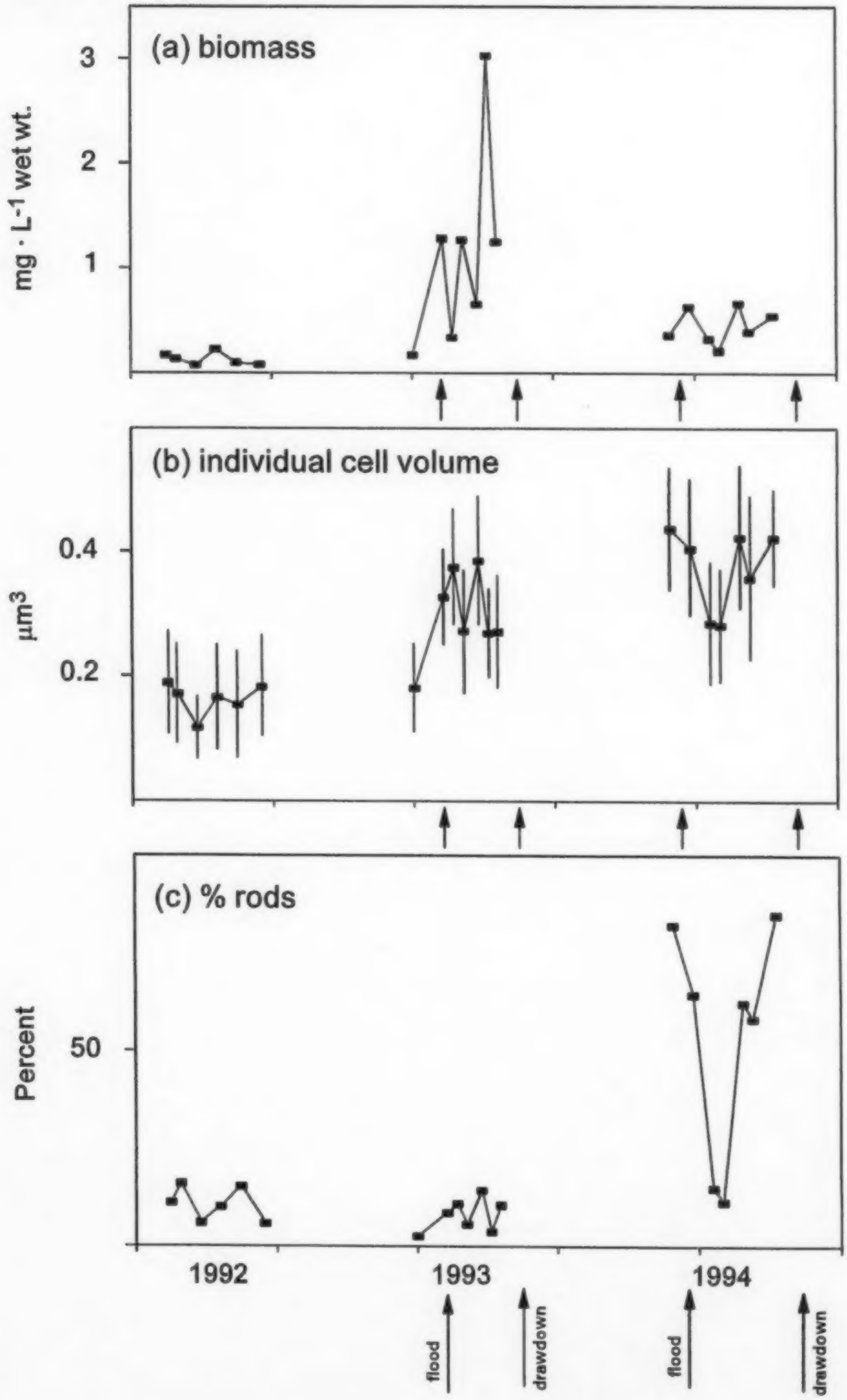


Fig. 7. (*a*) Changes in zooplankton biomass in Lake 979, 1992–1994. (*b*) Changes in zooplankton species composition in the original pond.

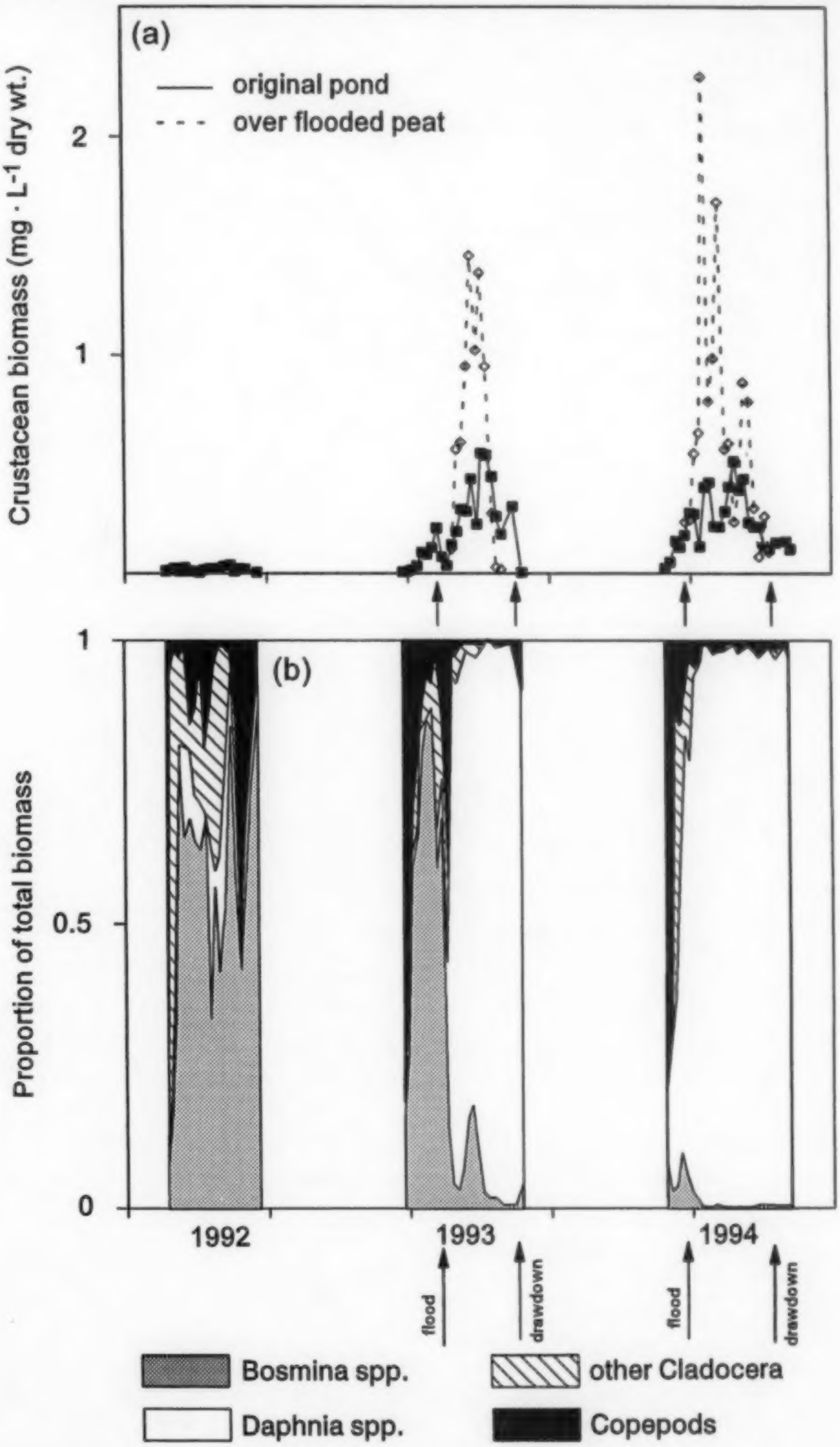
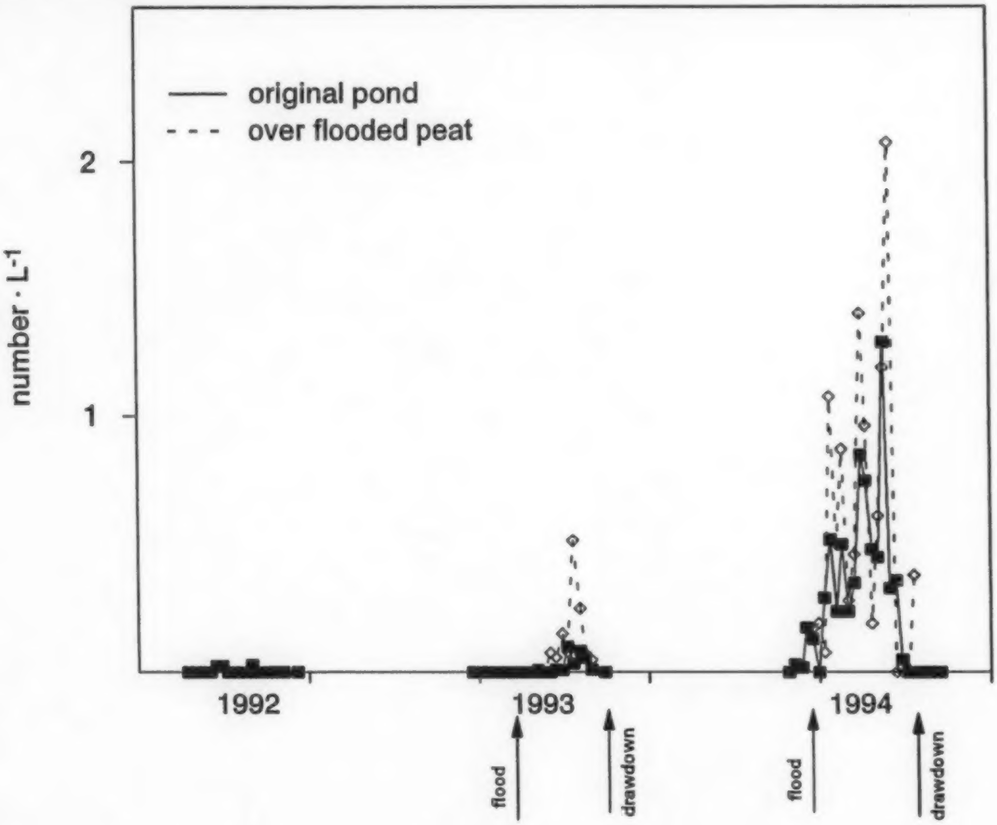


Fig. 8. Changes in densities of *Chaoborus* spp. in the original pond and over flooded peat, 1992–1994.



observed in Lake 979 are a chance occurrence unrelated to impoundment.

Flooding of Lake 979 initiated a series of rapid changes in the plankton community, and a new steady state was not achieved within the first 2 years of impoundment. Changes in plankton were apparently the result of alterations in hydrology, nutrient availability, and zooplankton grazing.

Hydrology

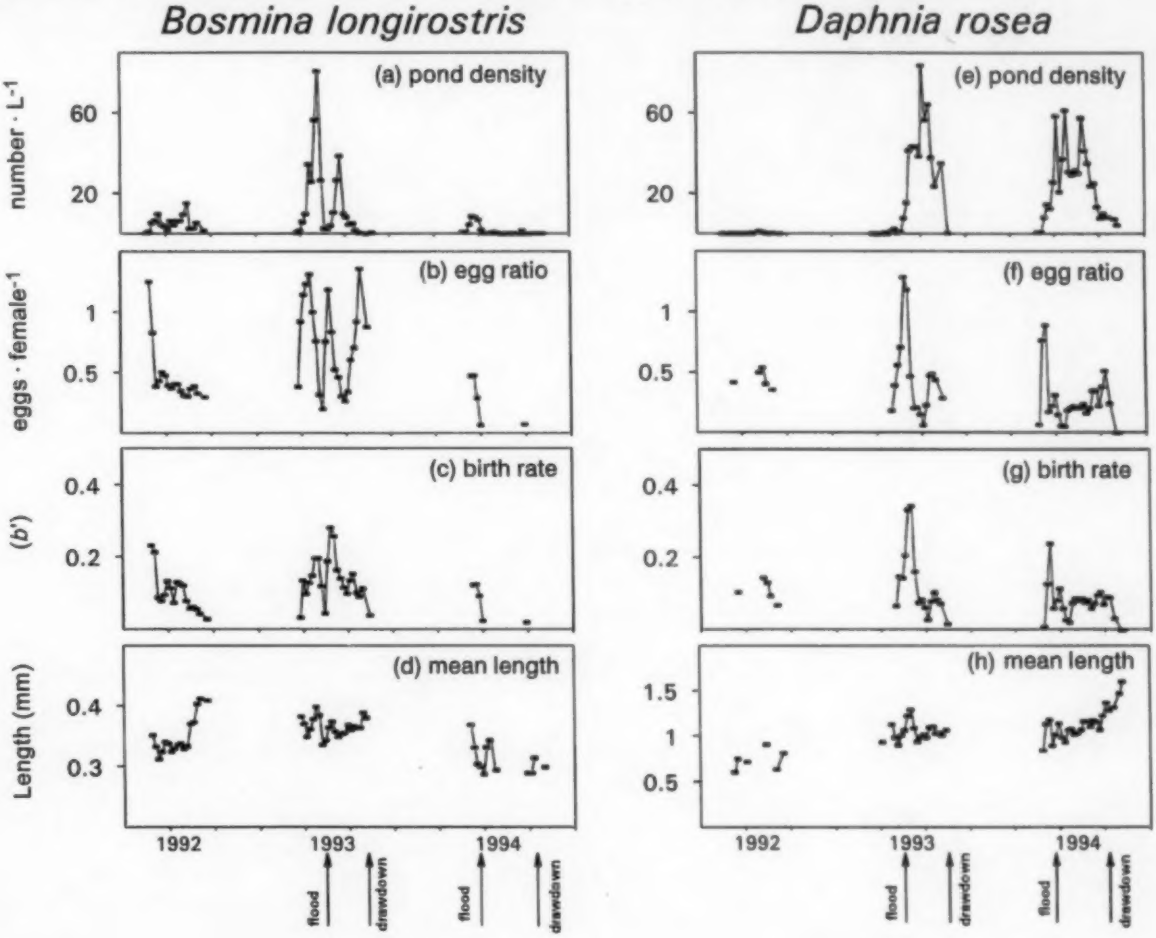
Throughout the study, levels of almost all chemical and biological parameters were correlated with hydrologic residence times, reflecting the dilution by inflows from Lake 240. The pond volume increased 7.4× after impoundment, and variations in residence times were less influential than in the preflooding period. After flooding, plankton dynamics were strongly affected by changes in hydrology only during short (2–3 week) periods immediately following impoundment and drawdown. At other times, water residence times usually exceeded the generation times of planktonic bacteria, phytoplankton, and zooplankton, and as a result, changes in hydrology did not strongly influence their population dynamics. Both before and during impoundment, per-capita losses to the outflow of zooplankton (the plankton group with the longest generation times) were always low relative to rates of birth, immigration from Lake 240, and in-pond mortality (M. Paterson, unpublished data).

The effect of impoundment on zooplankton

One of the most dramatic responses to impoundment was the large increase in zooplankton biomass and productivity. Several other studies have also observed increases in zooplankton biomass after the creation of new reservoirs (Roche 1964; Dzyuban 1979; Pinel-Alloul and Méthot 1984).

High post-flooding densities of zooplankton were apparently maintained by a combination of high food availability and low rates of mortality. Egg ratios of both *D. rosea* and *B. longirostris* increased immediately after impoundment suggesting that per-capita food availability was high at this time. After 4–6 weeks, egg ratios declined, presumably in response to density-dependent food limitation. The decline in birth rates may also have indicated a dietary switch from high-quality algae to lower quality bacteria (see below). Despite low birth rates, densities of *D. rosea* and *B. longirostris* remained high throughout the summer of 1993 suggesting that mortality was low. Per-capita predation on zooplankton may have decreased after impoundment because fish densities were "diluted" by the greater pond volume. Fish predation may have been further reduced by the presence of refugia created by low oxygen conditions over the flooded peat. The shift in zooplankton community composition from dominance by small species (*B. longirostris*) to dominance by larger species (*D. rosea*) is consistent with decreased size-selective predation by fish after impoundment.

Fig. 9. Changes in densities, egg ratios, birth rates (*b′*), and mean lengths of *B. longirostris* and *D. rosea* in Lake 979, 1992–1994.

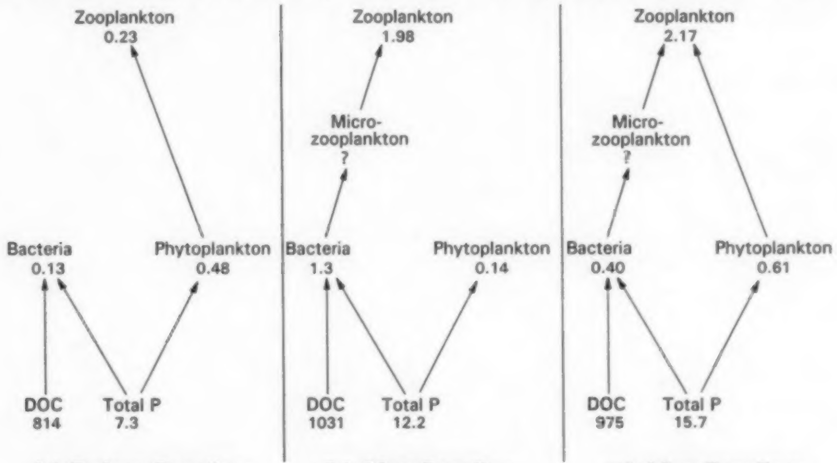


In 1994, *B. longirostris* numbers in Lake 979 fell dramatically. Low egg ratios in May 1994 suggest that the population was severely food limited, possibly as a result of competition between *B. longirostris* and *D. rosea.* High densities of *Chaoborus* were also present in 1994 and may have further contributed to the virtual elimination of *B. longirostris* from the pond.

Production of Cladocera at the centre buoy frequently equaled or exceeded phytoplankton production during impoundment in 1993. This suggests that zooplankton in Lake 979 could not obtain all of their energetic needs from phytoplankton. It is unlikely that this conclusion is a methodological artifact, despite limitations in our techniques. Our determinations of zooplankton productivity are underestimates because they do not include copepods, rotifers, or microzooplankton. The determinations of phytoplankton photosynthesis are also conservative (with respect to our conclusions) because ^{14}C techniques overestimate net phytoplankton production (Peterson 1980). Similar determinations of ecological efficiency (herbivore production/net primary production) in other lakes have usually found values between 5 and 15% (e.g., Coveney et al. 1977; Lewis 1979; Makarewicz 1985; M. Paterson, unpublished data). Hence, our estimates for Lake 979 (which exceeded 100%) would have to be in error by 10× or more to strongly affect our conclusions.

The most important post-flooding resource for zooplankton in 1993 was probably bacteria. After flooding, bacterial biomass exceeded phytoplankton biomass, and changes in cell volumes increased the susceptibility of bacteria to grazing by *Daphnia* (Geller and Müller 1981; Gophen and Geller 1984). Several studies suggest that bacterial growth rates increase with cell size (Simek 1986; Roszak and Colwell 1987; Currie 1990). When linked with greater biomass, this suggests that bacterial productivity increased greatly in Lake 979 during impoundment. Large increases in methane and CO_2 production following flooding of Lake 979 were observed by Kelly et al. (1997), providing a further indication of increased bacterial production. *Daphnia rosea* may have dominated the post-flooding zooplankton community because it is a better bacterial grazer than other zooplankton species present prior to flooding (Geller and Müller 1981; Hessen et al. 1989). Bacterial cell volumes may have increased in response to improved

Fig. 10. Schematic diagram of changes in mean concentrations of total P ($\mu g\cdot L^{-1}$), DOC ($\mu mol\cdot L^{-1}$), and biomass ($mg\cdot L^{-1}$ wet wt.) of different planktonic groups measured at the centre buoy in Lake 979 before and after flooding. Averages do not include data collected after drawdown. The solid arrows indicate speculative relationships among P, DOC, bacteria, phytoplankton, and zooplankton. Changes in the availability of labile DOC for bacteria are not known and, hence, are not depicted. Dry weights of zooplankton were assumed to be 15% of wet weights.



(a) Before flooding (1992-1993) (b) After flooding (1993) (c) After flooding (1994)

nutrient conditions (Roszak and Colwell 1987; Wiebe et al. 1992), decreased oxygen concentrations (Cole et al. 1993), or decreased size-selective predation by microzooplankton (Güde 1989; Chrzanowski and Simek 1990).

Taken together, the zooplankton, phytoplankton, and bacterial data suggest that the dominant pathway of carbon flow supporting higher trophic levels changed after flooding (Fig. 10). We postulate that zooplankton fed primarily on phytoplankton prior to impoundment (Fig. 10*a*). Bacterial production was apparently low and average cell volumes were at or below threshold sizes for zooplankton consumption (Gophen and Geller 1984). Changes in bacterial biomass and cell size after flooding increased their availability, and this resource apparently supported high levels of zooplankton production in 1993 (Fig. 10*b*). In 1994, bacterial biomass declined (although individual cell sizes were still large) and phytoplankton photosynthesis increased. As a result, the relative importance of bacteria and phytoplankton to zooplankton in the second year of flooding is uncertain (Fig. 10*c*).

Interactions of zooplankton and bacteria with phytoplankton

The response of the phytoplankton community to impoundment differed in 1993 and 1994. After flooding in 1993, both phytoplankton biomass and photosynthesis declined. In 1994, phytoplankton biomass and production increased after an initial decline in May.

It is likely that the decline of phytoplankton after impoundment in 1993 was primarily the result of greater grazing pressure by zooplankton. High densities of *D. rosea* were apparently maintained during periods of low algal abundance by high densities of edible bacteria. Aside from zooplankton grazing, there are suggestions that other factors further contributed to the decline of phytoplankton. After a brief increase following impoundment in June 1993, specific growth rates of phytoplankton (P_{m}^{B} and $P_{opt}\cdot B^{-1}$) decreased beginning in late July. This is surprising because TDP concentrations were high, and intense grazing should have reduced density-dependent nutrient limitation within the phytoplankton community (Sterner 1989). Phytoplankton biomass and photosynthesis increased in 1994 (relative to 1993) despite minimal changes in zooplankton densities and TDP concentrations. Mean annual biomass of bacteria and phytoplankton fluctuated reciprocally during the 3 years of study (Fig. 10).

There are several possible explanations for these observations. First, P released immediately after impoundment may have been bound to organic complexes that were unavailable to phytoplankton but could be utilized by bacteria. Second, phytoplankton may have been limited by nutrients other than P. For example, Guildford et al. (1987) found that binding of iron by DOC decreased phytoplankton growth rates in a reservoir in northern Manitoba. Finally, several laboratory studies suggest that bacteria can directly outcompete phytoplankton for P (Rhee 1972; Currie and Kalff 1984; Makarewicz 1985; Vadstein and Olsen 1989).

It is generally argued that bacteria do not strongly compete with phytoplankton for P in lakes because (*i*) natural bacteria are usually limited by C, whereas phytoplankton are usually limited by P (Currie 1990), and (*ii*) natural bacteria are more strongly limited by predation than are phytoplankton (Wright and Coffin 1984). In Lake 979, flooding may have released bacteria from both of these checks. Grazing by *D. rosea* may have reduced numbers of ciliates and nannoflagellates that feed heavily on bacteria. Abundance of these predators typically declines in the presence of *Daphnia* (Güde 1989). Carbon limitation of bacterial growth may also have been diminished by greater availability of DOC from flooded organic matter. DOC released immediately after flooding was probably highly labile and readily utilized by bacteria (Polunin 1984). Over time, the lability of leached DOC typically decreases (Polunin

1984), and bacteria in Lake 979 may once again have become C limited by 1994. This would increase P availability for phytoplankton and account for the higher algal densities observed in 1994. It is also possible that bacteria became increasingly limited by predation after 1993. The mechanisms underlying such a change are unclear.

Findlay et al. (1994) observed similar changes in numbers of bacteria and phytoplankton following manipulations of predatory fish in Lake 221 at ELA. They argued that reductions of microzooplankton by *Chaoborus*, an invertebrate predator, released bacteria from predatory control and caused greater competition between bacteria and phytoplankton. These results suggest that observations in Lake 979 may have implications for other systems.

Changes in zooplankton biomass in Lake 979 did not markedly affect phytoplankton size composition. This is surprising, because large increases in zooplankton grazing often result in greater proportional representation by large, inedible species of phytoplankton (Sterner 1989). It is generally argued that large phytoplankton are inferior competitors for nutrients because of their low surface area/volume ratios (Porter 1977). Hence, grazers can provide a niche for large, inedible algal species by selectively removing small algae and reducing density-dependent nutrient limitation (Sterner 1989). We speculate that large algae in Lake 979 did not increase after flooding because competition for nutrients was not diminished, despite large increases in grazing. Decreases in algal densities were offset by increases in bacteria, so that nutrient conditions for phytoplankton did not improve. Hence, the algal community could not shift towards a more grazer-resistant size structure, and phytoplankton were virtually eliminated from the pond.

In summary, impoundment of Lake 979 resulted in large changes in plankton productivity and community structure. Many of the most important changes were apparently the result of shifts within the bacterial community. Increases in bacterial biomass and cell sizes supported high densities of zooplankton, which in turn, reduced phytoplankton production and biomass. Increased competition for P with bacteria may have further decreased phytoplankton productivity. Greater consideration of changes in planktonic interactions involving bacteria should be given in the design of future food web experiments.

Acknowledgments

This research was supported by Manitoba Hydro and the Canadian Department of Fisheries and Oceans Habitat Action Plan. The ELARP project was coordinated by Drs. J. Rudd and C. Kelly. We thank all who assisted with the collection of samples including J. Embury, P. Gerrard, M. Lyng, C. Magura, and V. St.Louis. Drs. R. Bodaly, B. Hecky, C. Kelly, D. Rosenberg, J. Rudd, and V. St. Louis provided support and constructive criticism throughout the study. The ELA and Freshwater Institute Chemical Analytical Laboratories performed all chemical analyses. R. Bodaly, B. Hecky, L. Hendzel, R. Hesslein, D. Rosenberg, J. Rudd, V. St. Louis, A. Salki, H. Welch, and two anonymous reviewers provided useful comments on earlier drafts of this manuscript.

References

Adam, S.M., Kimmel, B.L., and Plosky, G.R. 1983. Sources of organic matter for reservoir fish production: a trophic-dynamics analysis. Can. J. Fish. Aquat. Sci. **40**: 1480–1495.

Allen, G., Yan, N.D., and Geiling, W.T. 1994. ZEBRA2—zooplankton enumeration and biomass routines for APIOS: a semi-automated sample processing system for zooplankton ecologists. Ontario Ministry of Environment and Energy, Toronto, Ont.

Andersen, T., and Hessen, D.O. 1991. Carbon, nitrogen, and phosphorus content of freshwater zooplankton. Limnol. Oceanogr. **36**: 807–814.

Anderson, D.H., and Benke, A.C. 1994. Growth and reproduction of the cladoceran *Ceriodaphnia dubia* from a forested floodplain swamp. Limnol. Oceanogr. **39**: 1517–1527.

Armstrong, F.A.J., and Schindler, D.W. 1971. Preliminary characterization of waters in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. **28**: 171–187.

Baxter, R.M., and Glaude, P. 1980. Environmental effects of dams and impoundments in Canada. Can. Bull. Fish. Aquat. Sci. No. 205.

Berman, T. 1985. Uptake of [^{32}P]orthophosphate by algae and bacteria in Lake Kinneret. J. Plankton Res. **7**: 71–84.

Canfield, D.E., Green, W.J., Gardner, T.J., and Ferdelman, T. 1984. Elemental residence times in Acton Lake, Ohio. Arch. Hydrobiol. **100**: 501–519.

Chrzanowski, T.H., and Simek, K. 1990. Prey-size selection by freshwater flagellated protozoa. Limnol. Oceanogr. **35**: 1429–1436.

Cole, J.J., Pace, M.L., Caraco, N.F., and Steinhart, G.S. 1993. Bacterial biomass and cell size distributions in lakes: more and larger cells in anoxic waters. Limnol. Oceanogr. **38**: 1627–1632.

Coveney, M.F., Cronberg, G., Enell, M., Larsson, K., and Olofsson, L. 1977. Phytoplankton, zooplankton and bacteria—standing crop and production relationships in a eutrophic lake. Oikos, **29**: 5–21.

Currie, D.J. 1990. Large-scale variability and interactions among phytoplankton, bacterioplankton, and phosphorus. Limnol. Oceanogr. **35**: 1437–1455.

Currie, D.J., and Kalff, J. 1984. A comparison of the abilities of freshwater algae and bacteria to acquire and retain phosphorus. Limnol. Oceanogr. **29**: 298–310.

Downing, J.A., Perusse, M., and Frenette, Y. 1987. Effect of interreplicate variance on zooplankton sampling design and data analysis. Limnol. Oceanogr. **32**: 673–680.

Duthie, H.C., and Ostrofsky, M.L. 1975. Environmental impact of the Churchill Falls (Labrador) hydroelectric project: a preliminary assessment. J. Fish. Res. Board Can. **32**: 117–125.

Dzyuban, N.A. 1979. The invertebrates: A. The zooplankton (metazoic) of the Volga. *In* The River Volga and its life. *Edited by* P.D. Mordukhai-Boltovskoi. Dr. W. Junk, Boston, Mass. pp. 195–231.

Fee, E.J., Shearer, J.A., DeBruyn, E.R., and Schindler, E.U. 1992. Effects of lake size on phytoplankton photosynthesis. Can. J. Fish. Aquat. Sci. **49**: 2445–2459.

Findlay, D.L., Kasian, S.E.M., Hendzel, L.L., Regehr, G.W., Schindler, E.U., and Shearer, J.A. 1994. Biomanipulation of Lake 221 in the Experimental Lakes Area (ELA): effects on phytoplankton and nutrients. Can. J. Fish. Aquat. Sci. **51**: 2794–2807.

Findlay, D.L., Kasian, S.E.M., and Schindler, E.U. 1996. Long-term effects of low cadmium concentrations on a natural phytoplankton community. Can. J. Fish. Aquat. Sci. **53**: 1903–1912.

Gannon, J.E., and Gannon, S.A. 1975. Observations on the narcotization of crustacean zooplankton. Crustaceana, **28**: 220–224.

Geller, W., and Müller, H. 1981. The filtration apparatus of Cladocera: filter mesh-sizes and their implications on food selectivity. Oecologia, **49**: 316–321.

Gliwicz, Z.M., and Boavida, M.J. 1996. Clutch size and body size at first reproduction in *Daphnia pulicaria* at different levels of food and predation. J. Plankton Res. **18**: 863–880.

Gophen, M., and Geller, W. 1984. Filter mesh size and food particle uptake by *Daphnia*. Oecologia, **64**: 408–412.

Güde, H. 1989. The role of grazing on bacteria in plankton succession. *In* Plankton ecology: succession in plankton communities. *Edited by* U. Sommer. Springer-Verlag, Berlin. pp. 337–364

Guildford, S.J., Healey, F.P., and Hecky, R.E. 1987. Depression of primary production by humic matter and suspended sediment in limnocorral experiments at Southern Indian Lake, northern Manitoba. Can. J. Fish. Aquat. Sci. **44**: 1408–1417.

Hessen, D.O., Andersen, T.O., and Lyche, A. 1989. Differential grazing and resource utilization of zooplankton in a humic lake. Arch. Hydrobiol. **114**: 321–347.

Jones, R.I. 1992. The influence of humic substances on lacustrine planktonic food chains. Hydrobiologia, **229**: 73–91.

Kelly, C.A., St. Louis, V.L., Scott, K.J., Dyck, B., Rudd, J.W.M., Bodaly, R.A., Roulet, N.R., Heyes, A., Moore, T.R., Schiff, S., Aravena, R., Warner, B., Harris, R., and Edwards, G. 1997. Increases in fluxes of greenhouse gases and methyl mercury following flooding of an experimental reservoir. Environ. Sci. Technol. In press.

Lewis, W.M. 1979. Zooplankton community analysis. Springer-Verlag. Berlin.

Makarewicz, J.C. 1985. Production and limiting factors. 5. Zooplankton. *In* An ecosystem approach to aquatic ecology. *Edited by* G.E. Likens. Springer-Verlag, New York. pp. 268–280.

Malley, D.F., Lawrence, S.G., MacIver, M.A., and Findlay, W.J. 1989. Range of variation in estimates of dry weight for planktonic Crustacea and Rotifera from temperate North American lakes. Can. Tech. Rep. Fish. Aquat. Sci. No. 1666.

McCauley, E. 1984. The estimation of the abundance and biomass of zooplankton in samples. *In* A manual on methods for the assessment of secondary productivity in fresh waters. *Edited by* J.A. Downing and F.H. Rigler. Blackwell Scientific, Oxford. pp. 228–265.

Nauwerck, A. 1963. Die beziehungen zwischen zooplankton und phytoplankton im See Erken. Symb. Bot. Ups. **17**: 1–163.

Ostrofsky, M.L. 1978. Trophic changes in reservoirs: an hypothesis using phosphorus budget models. Int. Rev. Gesamten Hydrobiol. **63**: 481–499.

Pace, M.L. 1984. Zooplankton community structure, but not biomass, influences the phosphorus – chlorophyll *a* relationship. Can. J. Fish. Aquat. Sci. **41**: 1089–1096.

Paloheimo, J.E. 1974. Calculation of instantaneous birth rate. Limnol. Oceanogr. **19**: 692–694.

Peterson, B.J. 1980. Aquatic primary productivity and the ^{14}C-CO$_2$ method: a history of the productivity problem. Annu. Rev. Ecol. Syst. **11**: 359–385.

Pinel-Alloul, B., and Méthot, G. 1984. Etude préliminaire des effets de la mise en eau du Réservoir de LG-2 (Territoire de la Baie James, Québec) sur le seston grossier et la zooplancton des rivières et des lacs inondés. Int. Rev. Gesamten Hydrobiol. **69**: 57–78.

Polunin, N.V.C. 1984. The decomposition of emergent macrophytes in fresh water. Adv. Ecol. Res. **14**: 115–166.

Porter, K.G. 1977. The plant–animal interface in freshwater ecosystems. Am. Sci. **65**: 159–170.

Porter, K.G., and Feig, Y.S. 1980. The use of DAPI for identifying and counting aquatic microflora. Limnol. Oceanogr. **25**: 943–948.

Rhee, G.Y. 1972. Competition between an alga and an aquatic bacterium for phosphate. Limnol. Oceanogr. **17**: 505–514.

Roche, W. 1964. Effects of impoundment on water chemistry and plankton in Lake Ransaren (Swedish Lappland). Verh. Int. Ver. Theor. Angew. Limnol. **15**: 437–443.

Romanenko, V.I. 1979. Microbiology of the Volga. *In* The River Volga and its life. *Edited by* P.D. Mordukhai-Boltovskoi. Dr. W. Junk, Boston, Mass. pp. 106–136.

Roszak, D.B., and Colwell, R.R. 1987. Survival strategies of bacteria in the natural environment. Microbiol. Rev. **51**: 365–379.

Salki, A.G. 1995. Lake variation and climate change study: crustacean plankton of a lake flushing rate series in the Experimental Lakes Area, northwestern Ontario, part 2, 1991–1993. Can. Data Rep. Fish. Aquat. Sci. No. 967.

Saunders, J.F., and Lewis, W.M. 1988. Dynamics and control mechanisms in a tropical zooplankton community (Lake Valencia, Venezuela). Ecol. Monogr. **58**: 337–353.

Schindler, D.W., and Novén, B. 1971. Vertical distribution and seasonal abundance of zooplankton in two shallow lakes of the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. **28**: 245–256.

Shearer, J.A. 1978. Two devices for obtaining water samples integrated over depth. Can. Fish. Mar. Serv. Tech. Rep. No. 772.

Simek, K. 1986. Bacterial activity in a reservoir determined by autoradiography and its relationship to phyto- and zooplankton. Int. Rev. Gesamten Hydrobiol. **71**: 593–612.

Stainton, M.P., Capel, M.J., and Armstrong, F.A.J. 1977. The chemical analysis of fresh water. 2nd ed. Can. Fish. Mar. Serv. Misc. Spec. Publ. No. 25.

Sterner, R.W. 1989. The role of grazers in phytoplankton succession. *In* Plankton ecology; succession in plankton communities. *Edited by* U. Sommer. Springer-Verlag, Berlin. pp. 107–170.

Tranvik, L.J. 1992. Allochthonous dissolved organic matter as an energy source for pelagic bacteria and the concept of the microbial loop. Hydrobiologia, **229**: 107–114.

Vadstein, O., and Olsen, Y. 1989. Chemical composition and phosphate uptake kinetics of limnetic bacterial communities cultured in chemostats under phosphorus limitation. Limnol. Oceanogr. **34**: 939–946.

Wiebe, W.J., Sheldon, W.M., and Pomeroy, L.R. 1992. Bacterial growth in the cold: evidence for an enhanced substrate requirement. Appl. Environ. Microbiol. **58**: 359–364.

Wright, R.T., and Coffin, R.B. 1984. Measuring microzooplankton grazing on planktonic marine bacteria by its impact on bacterial production. Microb. Ecol. **10**: 137–149.

Yan, N.D. 1986. Empirical prediction of crustacean zooplankton biomass in nutrient-poor Canadian Shield lakes. Can. J. Fish. Aquat. Sci. **43**: 788–796.

Summer growth patterns of northern Dolly Varden (*Salvelinus malma*) smolts from the Prudhoe Bay region of Alaska

Robert G. Fechhelm, James D. Bryan, William B. Griffiths, and Larry R. Martin

Abstract: Summer length growth patterns of northern Dolly Varden (*Salvelinus malma*) smolts from the Sagavanirktok River, northern Alaska, were analyzed for the years 1985–1994 and found to be sigmoidal, indicating slow rates of growth in early and late summer with the most rapid growth occurring in midseason. Nonlinear logistic regression functions of mean cohort length against date provided a reasonable fit of the data for all years except for 1991, accounting for more than 94% (r^2 values ranged from 0.95 to 0.99) of the variation in mean daily length in any given year. Slow growth in early summer is in direct contrast with the growth patterns reported for juvenile broad whitefish (*Coregonus nasus*) and Arctic cisco (*C. autumnalis*) which inhabit the Sagavanirktok River and estuary. Some possible explanations for the observed Dolly Varden growth patterns include migration, dispersal, prey availability, water quality, and stock mixing.

Résumé : La croissance en longueur durant l'été des smolts de Dolly Varden septentrional (*Salvelinus malma)* de la rivière Sagavanirktok, dans le nord de l'Alaska, pour les années 1985–1994 a été étudiée. On a constaté une courbe de croissance de forme sigmoïde, indiquant un taux de croissance lent au début et à la fin de l'été et une croissance maximale au milieu de la saison. Des fonctions de régression logistique non linéaire de la longueur moyenne des cohortes par rapport à la date ont donné un ajustement raisonnable des données pour toutes les années sauf 1991, expliquant plus de 94 % (valeurs de r^2 variant entre 0,95 et 0,99) de la variation de la longueur quotidienne moyenne dans toutes les années étudiées. Une croissance lente au début de l'été s'oppose directement aux observations faites sur la croissance du corégone tschir (*Coregonus nasus)* et du cisco arctique (*C. autumnalis*) vivant dans la rivière Sagavanirktok et son estuaire. Certaines explications possibles des particularités de la croissance du Dolly Varden comprennent la migration, la dispersion, la disponibilité des proies, la qualité de l'eau et le mélange des stocks.

[Traduit par la Rédaction]

Introduction

The northern form of the amphidromous Dolly Varden[1] (*Salvelinus malma*) spawns in many of the larger river systems of the Alaskan/Canadian Beaufort Sea (Craig 1984; Everett and Wilmot 1987). The presence of perennial springs appears to be a prerequisite for spawning in these arctic rivers, most likely because they provide fish with open-water habitat throughout the winter (Craig 1984). Juveniles remain within their natal streams for several years prior to their first seaward migration to food-rich coastal waters (Craig 1977*a*, 1977*b*, 1989). After smolting, Dolly Varden generally exhibit an amphidromous life history strategy wherein they disperse out into coastal waters to feed each summer and then return upriver to overwinter (Craig 1989). There is also a component of the population that consists of nonamphidromous males that remain within their natal rivers for their entire life (Craig 1977*a*, 1977*b*, 1989). Amphidromous Dolly Varden migrate considerable distances along the coast during the summer, and although spawners are believed to maintain fidelity to their natal streams, nonspawners may overwinter in nonnatal drainages (Glova and McCart 1974; Craig 1977*a*; DeCicco 1985, 1992).

Because the summer feeding foray into coastal waters is a time of intense feeding and growth, it represents an important phase in the yearly life cycle of Beaufort Sea Dolly Varden (Craig 1989). Yet, little is known of the fine-scale summer growth patterns or feeding ecology of these arctic populations. Two whitefish species abundant in the Alaskan Beaufort Sea, the amphidromous broad whitefish (*Coregonus nasus*) and the anadromous Arctic cisco (*C. autumnalis*), exhibit summer growth patterns that are closely associated with coastal water temperatures (Fechhelm et al. 1992, 1995; Griffiths et al. 1992). Growth is fastest early in the open-water season when nearshore water temperatures are their highest, but then declines in apparent conjunction with decreasing water temperature as the summer progresses.

This paper analyzes summer length growth patterns of northern Dolly Varden smolts from the Sagavanirktok River, Alaska, for the years 1985–1994. The Sagavanirktok River supports one of the larger Dolly Varden populations on the Alaskan North Slope (McCart and Craig 1971; Yoshihara 1972; Furniss 1975; Bendock 1983). Growth patterns are compared with those of broad whitefish and Arctic cisco from the

Received June 14, 1996. Accepted October 7, 1996.
J13507

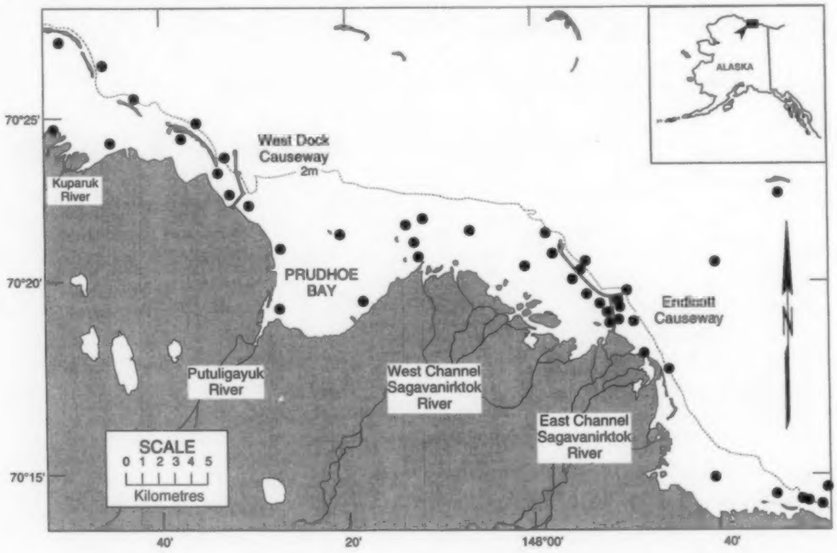
R.G. Fechhelm,[2] J.D. Bryan, and L.R. Martin. LGL Ecological Research Associates, Incorporated, 1410 Cavitt Street, Bryan, TX 77801, U.S.A.
W.B. Griffiths. LGL Limited Environmental Research Associates, 9768 Second Street, Sidney, BC V8L 3Y8, Canada.

[1] Fish of the genus *Salvelinus* caught along the Beaufort Sea coast prior to the mid-1980s were identified as the western Arctic Bering Sea form of the Arctic char (*S. alpinus*). Morrow (1980) and Behnke (1980, 1984) contend that these fish are northern forms of the Dolly Varden (*S. malma*). This paper conforms to the latter taxonomic designation.

[2] Author to whom all correspondence should be addressed.

Can. J. Fish. Aquat. Sci. **54**: 1103–1110 (1997)

Fig. 1. Prudhoe Bay and Sagavanirktok River delta region of the Alaskan Beaufort Sea. Sampling locations for 1985–1994 are indicated by solid circles. Not all sites were sampled each year.



same region. Life history and ecological facets of Beaufort Sea Dolly Varden are examined.

Methods

Dolly Varden were collected in fyke nets located in the vicinity of Prudhoe Bay and the Sagavanirktok River delta during the summers of 1985–1994 (Fig. 1). Surveys were conducted during the open-water season which typically lasted from late June into September. Except for periods of inclement weather, sampling continued on a 24 h basis throughout the summer with nets being serviced approximately the same time each day. Captured fish were placed into floating holding pens, anesthetized in a dilute solution of tricaine methanesulfonate (MS 222), measured (fork length in millimetres), and then released after the effects of the anesthetic had worn off.

A consistent feature of the length–frequency profile of northern Dolly Varden collected in the Prudhoe Bay area is the presence of a dominant size cohort characterized by a modal length of approximately 150–160 mm in early summer growing to 200–240 mm by late August (Fig. 2). The examples depicted in Fig. 2 were arbitrarily chosen to illustrate the presence of this size cohort; however, this feature was characteristic of all 10 years. Because Dolly Varden smaller than this cohort are rare in coastal waters, fish from this size group probably represent recently smolted fish undergoing their initial seaward migration. Similar-sized smolts (e.g., 120–160 mm) have been reported for northern Dolly Varden from northwestern Alaska (DeCicco 1990). Otolith aging of Sagavanirktok River Dolly Varden in 1995 ($N = 14$) indicated that fish from this size group were primarily 2- and 3-yr-old fish. This smolt cohort was isolated by inspection of length–frequency profiles and served as the basis for our analysis. The underlying premise was that this group represented a distinct size cohort, the mean length of which could be tracked daily throughout the course of each summer.

Preliminary examination of plots of mean cohort length by date revealed growth patterns that appeared curvilinear and monotonically increasing. A nonlinear logistic regression function (Neter et al. 1989) was therefore used to initially fit the data (i.e., mean cohort length against day number) for each year:

$$Y_i = \beta_2 + \beta_3\cdot((\exp(\beta_0 + \beta_1 X_i))/(1 + \exp(\beta_0 + \beta_1 X_i)))$$

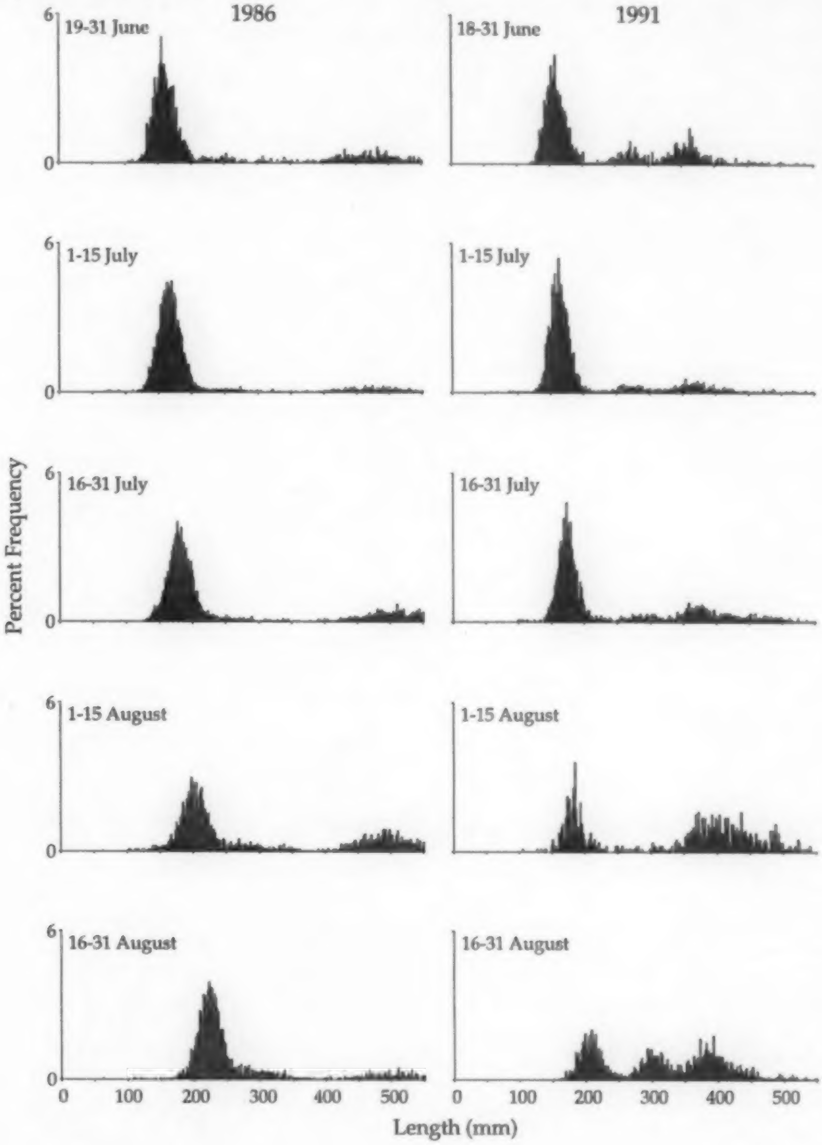
where X_i is mean daily cohort length, β_0 and β_1 are the curve parameters, β_2 is the start length parameter, and β_3 is the parameter that estimates change in daily mean length ($\beta_2 + \beta_3$ = asymptotic length estimate). Parameter values were estimated using the quasi-Newton method (Wilkinson 1989). This approach uses estimates of first and second derivatives to minimize the model's loss function via iteration. For each year, initial parameter estimates were determined by inspection of the length-at-date data. For modelling purposes, dates were quantified by numerically indexing them as consecutive integers standardized to June 15 = day 1 for all years. Growth for 1992 was not analyzed because midsummer catch data were insufficient for detecting a continuous length trend throughout the entire summer.

Results and discussion

Logistic regression functions of mean length against date provided a reasonable fit of the data for all years except for 1991, accounting for 95–99% of the variation in mean daily length in any given year (Table 1; Fig. 3). Regression functions were also derived using individual fish lengths instead of mean cohort length, but as would be expected, r^2 values decreased precipitously due to the additional variation in the lengths among individual fish. No meaningful logistic regression model could be derived for the 1991 data because of the absence of an asymptote that year. Whether this phenomenon reflected a real biological event or merely a data anomaly (e.g., weak and variable late summer catch) is unknown. However, both linear ($P \leq 0.001$, $r^2 = 0.90$) and second-order polynomial ($P \leq 0.001$, $r^2 = 0.92$) regressions (Neter et al. 1989) provided reasonable fits for the 1991 data, thereby providing some quantitative evidence of growth that year.

The logistic models indicate a slow rate of growth for Dolly Varden smolts early in the summer, rapid growth in midseason, and a slowing growth rate in the latter part of August and early September. The apparent cessation of growth in late summer may be linked to a shift in the Dolly Varden's ecological strategy. Seasonal catch-per-unit-effort (CPUE: fish per net

Fig. 2. Length–frequency distributions (≤550 mm) for Dolly Varden during the summers of 1986 and 1991. Data for these years were arbitrarily chosen to show the dominance of the smolt cohort in the overall length–frequency distribution. This cohort was clearly discernable in the length–frequency profile in all 10 years.



per 24 h) of smolts in the coastal waters of Prudhoe Bay and the Sagavanirktok River delta is typically bimodal, with the highest catch rates occurring early and late in the summer interspersed with a notable midsummer decrease in catch (Fig. 4). We believe that this pattern represents the early-summer outmigration from overwintering areas in the Sagavanirktok River (high early-summer catch), dispersal away from the immediate sampling area, possibly along the coast and (or) out to sea (midsummer lows in CPUE), and a late-summer return migration (high late-summer catch). A shift from a feeding strategy to a migratory strategy could account for the late-summer reduction in feeding (and growth) as fish begin returning to overwintering areas.

The slow rate of growth observed in early summer from June through mid-July is in direct contrast with the growth patterns of juvenile broad whitefish and Arctic cisco which also inhabit the Sagavanirktok River and estuary (Fig. 5). Both coregonid species consistently exhibit overall growth trends that are hyperbolic, with growth rates being greatest in early summer but that progressively decrease during the course of the open-water season (Fechhelm et al. 1992, 1995; Griffiths et al. 1992). Nearshore water temperature, which generally

Table 1. Summary results of nonlinear logistic regressions of mean length against date (N = number of days).

Year	N	β_0	β_1	β_2	β_3	r^2
1985	87	−4.33	0.09	159.07	74.70	0.98
1986	88	−3.47	0.07	152.08	80.45	0.99
1987	83	−5.18	0.09	154.28	87.27	0.97
1988	71	−5.08	0.11	151.07	74.60	0.95
1989	55	−5.97	0.12	163.90	94.07	0.96
1990	68	−4.95	0.10	160.45	94.56	0.96
1991	71	—	—	—	—	—
1993	76	−6.12	0.13	155.05	87.13	0.96
1994	63	−5.75	0.11	161.36	99.09	0.96

Note: No meaningful regression model could be derived for the 1991 data.

decreases throughout the summer from early-season highs, has been strongly implicated as a prime factor controlling the growth of both coregonids. Obviously, the prey resources upon which the whitefish species depend must be at sufficient levels to support their high early-summer growth rates. The relationships described for Arctic cisco and broad whitefish naturally prompted the question as to the effect of similar biotic and (or) abiotic factors on the growth patterns observed for Dolly Varden smolts.

Early-summer feeding studies conducted in the Sagavanirktok River delta area during 1986 and 1987 provide some evidence of different feeding strategies among the whitefish and Dolly Varden (Table 2). Results indicated that juvenile Arctic cisco rely on three primary food sources early in the summer (i.e., Chironomidae (Diptera midges), *Diaporeia affinis* (Amphipoda; originally referred to as *Pontoporiea affinis*, see Moulton et al. 1986; Cannon et al. 1987*a*; Knutzen et al. 1990*a*; Knutzen and Jewett 1991*a*), and *Mysis* spp.), while juvenile broad whitefish exploit two (i.e., Chironomidae and *D. affinis*). The absence of *Mysis* spp. in the diets of broad whitefish is commonly reported (Moulton et al. 1986; Cannon et al. 1987*a*) and may reflect ecological, morphological, or behavioral characteristics. In comparison, Chironomidae were not a major component in the diet of Dolly Varden, although other invertebrate species were represented. Predation appears highly selective because chironomid larvae are one of the least abundant invertebrate fauna found in the delta (Cannon et al. 1987*b*; Knutzen at al. 1990*b*; Knutzen and Jewett 1991*b*). If these data are truly indicative of early-summer trophic patterns in the delta region, then chironomids constitute a major dietary resource for Arctic cisco and broad whitefish at a time when summer growth rates are maximal for the two species. While it may be possible to compensate for this lost resource by feeding more heavily on other invertebrate fauna, the fact remains that Dolly Varden, for whatever reason, do not exploit this trophic resource which forms such a dominant component in the early-season growth of both coregonid species. To what extent this might contribute to the slow growth of Dolly Varden in early summer remains to be determined.

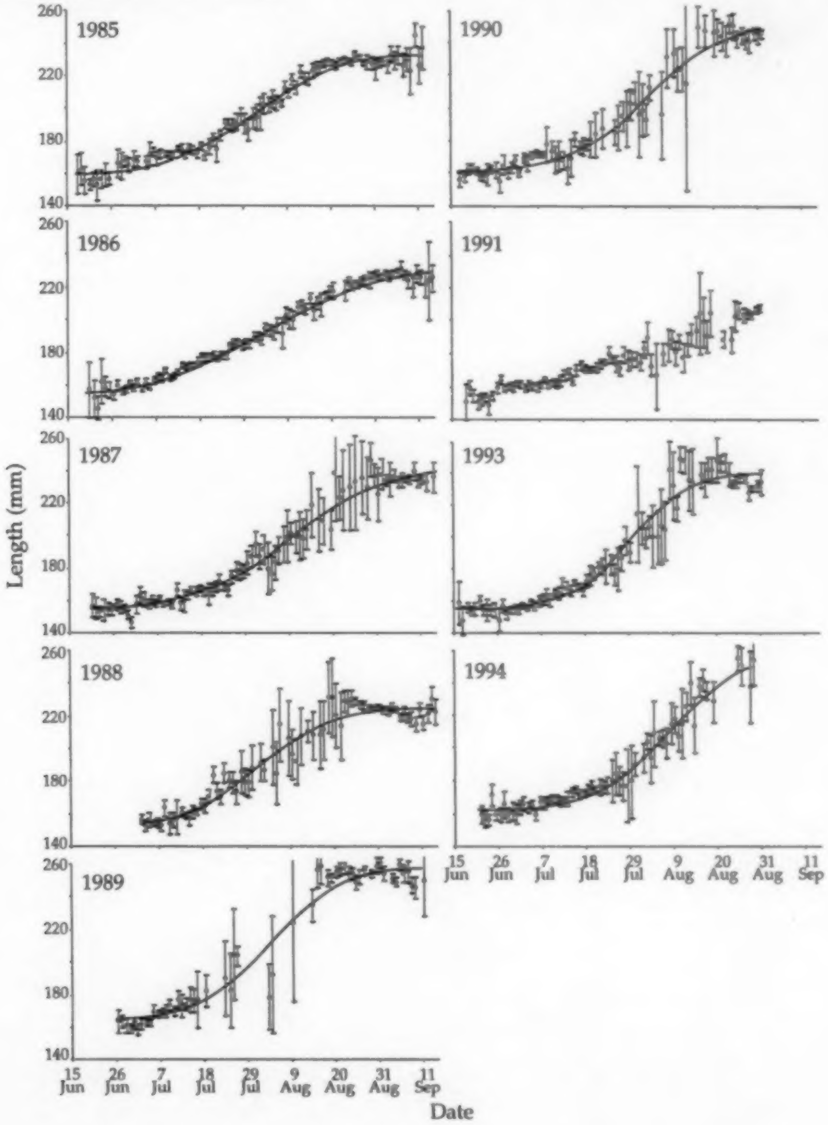
Another factor that might account for the slow growth of Dolly Varden smolts in early summer is the hydrographic condition of the delta and other nearshore areas along the Beaufort Sea coast. Arctic char from the Vardnes River in northern Norway exhibit an inverse relationship between seasonal growth and water temperature, a trend that prompted speculation that adaptation to arctic conditions allows these fish to grow best at low temperatures (Berg and Berg 1989). If similar adaptations are prevalent in the congeneric northern Dolly Varden, then growth rates would be expected to be poorest early in the summer when coastal water temperatures are at their highest. As the summer progresses, the continuous mixing of warm, brackish nearshore water and cold offshore marine water causes coastal water temperatures to decline and salinities to increase (Niedoroda and Colonell 1990). Increasing growth with decreasing temperature could merely reflect a species-specific adaptation to an arctic existence. A strong association between growth patterns and the nearshore thermal cycle presumes that Dolly Varden are indeed restricted to nearshore coastal waters as opposed to venturing out into the perpetually cold offshore marine environment.

Migration to nearshore or offshore areas more suitable for feeding and growth may also be a factor contributing to the observed pattern of slow growth in early summer and rapid growth in midsummer. The midsummer low in fyke-net catch certainly indicates that Dolly Varden largely vacate the Prudhoe Bay and the Sagavanirktok River delta sampling area. It is well documented that northern Dolly Varden throughout Alaska undergo extensive alongshore and open-water migrations during summer (Glova and McCart 1974; Craig 1977*a*; Craig and Haldorson 1981; DeCicco 1985, 1992; Underwood et al. 1995) and are therefore quite capable of exploiting large segments of coastal habitat. Fish could be migrating to other nearshore habitats of enhanced coastal upwelling and productivity or to offshore waters, either of which might be characterized by higher prey abundance and (or) abiotic factors (e.g., temperature) that enable greater bioenergetic efficiency. Areas of high prey abundance are temporally and spatially patchy in both coastal and offshore waters (Craig et al. 1984), and the summer dispersal would enhance encounters with these prime feeding habitats. The net effect of smolts outmigrating through the delta sampling area would be the perception of slow cohort growth in early summer; fyke nets would be sampling a constant passage of nonfeeding/nongrowing smolts enroute to prime feeding areas. The vanguard of the outmigrating population may even enter a rapid growth phase far earlier than the overall growth curves suggest. Differences in the timing of the outmigration among different spawning aggregates or year classes could have a similar affect.

Whether Dolly Varden regularly feed offshore in the Beaufort Sea is unclear. Direct evidence of a major offshore dispersal is limited, since few Beaufort Sea fishery surveys have been conducted offshore with gear capable of taking this strong-swimming fish. Although adult Dolly Varden have been taken 8 km ($N = 34$) and 15 km ($N = 3$) offshore by fyke net (LGL 1990) and 5 km ($N = 34$) offshore by purse seine (Thorsteinson et al. 1990), there is no record of smolt-sized fish from offshore surveys.

There are indirect indications of offshore dispersal. Feeding studies conducted in 1985 reported that the amphipod *Apherusa glacialis* was the major component in the diet of Dolly Varden collected by fyke net in the last half of August (Cannon et al. 1987*a*). These fish included smolt-sized individuals 200–250 mm in length. *Apherusa glacialis* is a pelagic amphipod that is considered to be a member of ice biocenes, ecological communities that are associated with the underside of ice floes (Barnard 1959; Golikov and Averincev 1977; Griffiths and Dillinger 1981). Yet, while *A. glacialis* was the dominant prey, Stringer (1987) reported that from 11 August

Fig. 3. Daily mean (± 2 SE) fork lengths for Dolly Varden smolts collected during the 1985–1994 studies. Logistic regression functions fitted to mean daily cohort length are superimposed for each year.



until freeze-up on 15 September, ice floes remained in excess of 8 km seaward of the 2-m isobath (see Fig. 1). *Apherusa glacialis* was again conspicuous in the diet of smolt-sized Dolly Varden collected during the first 2 weeks of September 1986 (Knutzen et al. 1990*a*). Schrader and Hachmeister (1990) reported that Stefansson Sound was completely free of ice by 27 July of that year and that freeze-up did not begin until 26 September. The implication is that Dolly Varden smolts may have been offshore feeding amongst the ice floes.

The fact that adult northern Dolly Varden undergo extensive alongshore and open-water migrations during summer (Glova and McCart 1974; Craig 1977*a*; Craig and Haldorson 1981; DeCicco 1985, 1992; Underwood et al. 1995) is evidence that this species is far more tolerant of cold, saline conditions than the other anadromous and amphidromous species of the region. Whether smolts exhibit the same degree of marine tolerance is unknown. Catch data from Prudhoe Bay suggest that smolts readily disperse away from estuarine areas, but this dispersal could be primarily along the coast and not out to sea. On the other hand, cold adaptation could make offshore feeding more preferable both in terms of bioenergetics and trophic competition. Dolly Varden would not be competing for prey with the dominant whitefish species whose coastal distribution seems limited to warmer, brackish areas nearshore and in the vicinity of river estuaries. The ability to forage offshore would be additionally advantageous for larger piscivorous Dolly Varden in

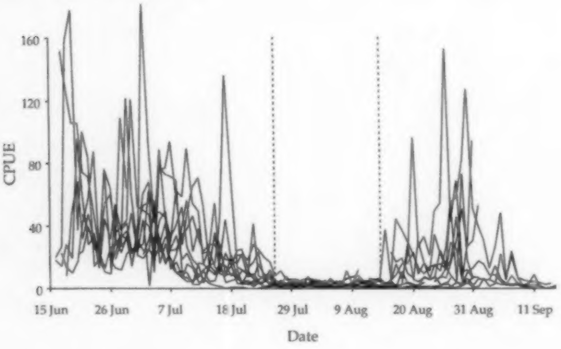
Table 2. Summary results of feeding studies conducted early (July) in the summers of 1986 and 1987.

	1986			1987		
Taxon	Arctic cisco $N = 15$	Broad whitefish $N = 13$	Dolly Varden $N = 22$	Arctic cisco $N = 46$	Broad whitefish $N = 20$	Dolly Varden $N = 43^a$
Chironomidae	29.7	55.7	0.1	33.3	98.3	10.4
Diaporeia affinis	20.1	41.2	48.8	35.4	1.4	53.7
Mysis spp.	50.2	—	17.2	30.7	—	10.0
Onisimus spp.	—	—	6.2	—	—	8.5
Polychaeta	—	—	22.6	—	—	—
Isopoda	—	—	—	—	—	10.0
Gammaracanthus loricatus	—	—	—	—	—	6.1
Other	0.0	3.1	5.1	0.6	0.3	1.3

Note: Data are limited to juvenile Artic cisco (≤150 mm), juvenile broad whitefish (≤150 mm), and Dolly varden smolts (≤200 mm) collected in the Sagavanirktok River delta and eastern Prudhoe Bay. Data are expressed in terms of percentage of total wet weight biomass. Sources: Knutzen et al. (1990*a*) and Knutzen and Jewett (1991*a*).

[a] A single fish that had been feeding heavily on Euphasiacea was not included.

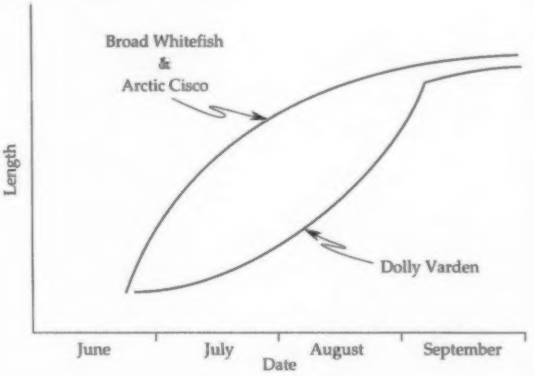
Fig. 4. Composite profile of yearly CPUE (fish per net per 24 h) for Dolly Varden smolts by date. Broken lines denote the midsummer decline in fyke-net catch.



that it would enable them to exploit standing stocks of Arctic cod (*Boreogadus saida*) that are so prevalent in arctic waters (Walters 1955; Morrow 1980).

A final consideration is the role that Dolly Varden smolts from neighboring river systems might have on length profiles observed in the Prudhoe Bay region. High catch rates during breakup in June most likely represent fish outmigrating from the Sagavanirktok River. But as the summer progresses, smolts dispersing from nearby populations may begin intermingling with Sagavanirktok River fish. Spawning populations are as close as 20 km east of the study area in the Shaviovik River (Craig 1984). The proportion of non-Sagavanirktok River fish in mid- and late-summer fyke-net catches is unknown as is their effect on the size structure of the smolt cohort. If, however, the inclusion of nonnatal smolts greatly alters growth profiles observed in the Prudhoe Bay area, it would imply that the different Dolly Varden populations along the Beaufort Sea coast have unique and distinctly different size structures and ecologies. If this were the case and given the relative consistency of the sigmoid growth curves over the decade, it would not be unreasonable to expect similar consistency in intrastock size variability. The occurrence of distinct stock differences among such geographically proximate populations is questionable but not impossible.

Fig. 5. Generalized summer growth patterns for Dolly Varden smolts, juvenile broad whitefish, and juvenile Arctic cisco. Data for broad whitefish and Arctic cisco are from Fechhelm et al. (1992, 1995) and Griffiths et al. (1992).



In summary, the observed summer growth patterns of Dolly Varden smolts from the Sagavanirktok River are decidedly different from those observed for juvenile broad whitefish and Arctic cisco. Whereas whitefish growth is most rapid in early summer when nearshore coastal water temperatures are highest, Dolly Varden growth rates do not reach their maxima until midsummer. This delayed onset of rapid growth may reflect migration to prime feeding areas in offshore waters or at other nearshore locations along the Beaufort Sea coast. Cold adaptation may also play a role in maximizing bioenergetic efficiency in the marine environment or in areas of strong coastal upwelling. Although the exact mechanisms responsible for the observed summer growth patterns remain to be determined, data indicate that anadromous Dolly Varden from the Beaufort Sea have adapted a life history strategy that minimizes trophic competition with the region's two other most abundant anadromous/amphidromous species.

Acknowledgments

We thank J. Erwin and G. Hubbard for critically reviewing the manuscript. We are also grateful to field managers D. Schmidt and R. Dillinger, senior field crew leaders B. Seavey and K. Waggoner, field team leaders G. Colonell, G. Lawley, and D. Malone, and field technicians T. Akpik, R. Basi, M. Bingham, S. Davis, L. Dugan, P. Fitzgerald, D. Gerkin, T. Green, B. Haley, A. Herrera, D. Hopler, J. Itta, S. Kilmowski, E. Parsons, B. Pierson, D. Rentenaar, D. Rosenau, and E. Westlien for their superb efforts during the 1988–1994 studies. Environmental monitoring programs were funded by the Endicott Development owners which is operated by BP Exploration (Alaska) Inc. Programs conducted from 1985 to 1987 were under the joint supervision of the Alaska Department of Fish and Game, the U.S. Environmental Protection Agency, the National Marine Fisheries Service, the North Slope Borough (NSB), the U.S. Army Corps of Engineers, and the U.S. Fish and Wildlife Service. Environmental monitoring programs from 1988 to 1994 were conducted under permit requirements and supervision of the NSB and the NSB Science Advisory Committee. The conclusions and opinions expressed in this paper do not necessarily represent those of any of the above-mentioned organizations.

References

Barnard, J.L. 1959. Epipelagic and under-ice Amphipoda of the Central Arctic Basin. Geophys. Res. Pap. **63**: 115–152.

Behnke, R.J. 1980. A systematic review of the genus *Salvelinus*. Charrs: salmonid fishes of the genus *Salvelinus*. *Edited by* E.K. Balon. Dr. W. Junk Publishers, The Hague, The Netherlands. pp. 441–480.

Behnke, R.J. 1984. Organizing the diversity of the Arctic charr complex. *In* Biology of the Arctic charr. Proceedings of the International Symposium on Arctic Charr, Winnipeg, Manitoba, May 1981. *Edited by* L. Johnson and B.L. Burns. University of Manitoba Press, Winnipeg. pp. 3–21.

Bendock, T. 1983. Inventory and cataloging of arctic area waters. Alaska Dep. Fish Game Annu. Rep. Fed. Aid Fish Res. Anadromous Fish Stud. **24**: 1–28.

Berg, O.K., and Berg, M. 1989. Sea growth and time of migration of anadromous Arctic char (*Salvelinus alpinus*) from the Vardnes River, in northern Norway. Can. J. Fish. Aquat. Sci. **46**: 955–960.

Cannon, T.C., Brancato, M.S., and Jewett S.C. 1987*a*. Fish food habits. Vol. 7, Chap. 3. *In* 1985 Endicott Environmental Monitoring Program. Report by Envirosphere Company to U.S. Army Corps of Engineers, Alaska District, Anchorage, Alaska. (Available from Envirosphere Company, 10900 8th St., Bellevue, WA 98004-4405)

Cannon, T.C., Brancato, M.S., and Jewett, S.C. 1987*b*. Fish prey surveys. Vol. 7, Chap. 4. *In* 1985 Endicott Environmental Monitoring Program. Report by Envirosphere Company to U.S. Army Corps of Engineers, Alaska District, Anchorage, Alaska. (Available from Envirosphere Company, 10900 8th St., Bellevue, WA 98004-4405.)

Craig, P.C. 1977*a*. Ecological studies of amphidromous and resident populations of Arctic char in the Canning River drainage and adjacent coastal waters of the Beaufort Sea, Alaska. Arctic Gas Biol. Rep. Ser. 41.

Craig, P.C. 1977*b*. Fisheries research in the Shaviovik Drainage, Alaska, with emphasis on Arctic char in the Kavik River. Arctic Gas Biol. Rep. Ser. 41.

Craig, P.C. 1984. Fish use of coastal waters of the Alaskan Beaufort Sea: a review. Trans. Am. Fish. Soc. **113**: 265–282.

Craig, P.C. 1989. An introduction to anadromous fishes in the Alaska arctic. Biol. Pap. Univ. Alaska, **24**: 27–54.

Craig, P.C., and Haldorson, L. 1981. Beaufort Sea barrier-island lagoon ecological process studies: Simpson lagoon. Part IV. *In* Environmental assessment of the Alaskan continental shelf. BLM/NOAA OCSEAP Boulder, Co. No. 7. pp. 384–678.

Craig, P.C., Griffiths, W.B., and Johnson, S.R. 1984. Trophic dynamics in an arctic lagoon. *In* The Alaskan Beaufort Sea: ecosystems and environments. *Edited by* P.W. Barnes, D.M. Schell, and E. Reimnitz. Academic Press, New York. pp. 347–380.

DeCicco, A.L. 1985. Inventory and cataloging of sport fish and sport fish waters of western Alaska with emphasis on Arctic char life history. Annual Report, 1984–1985. Alaska Dep. Fish Game Fed. Aid Res. **26**: 41–134.

DeCicco, A.L. 1990. Life history of anadromous Dolly Varden (*S. malma*) in northwestern Alaska. Int. Soc. Arctic Char Fanatics, 16–22 Sept., Murmansk, Russia.

DeCicco, A.L. 1992. Long-distance movements of anadromous Dolly Varden between Alaska and the U.S.S.R. Arctic, **45**: 120–123.

Everett, R.J., and Wilmot, R.L. 1987. Population genetic structure of Arctic char (*Salvelinus alpinus*) from rivers of the North Slope of Alaska. U.S Dep. Commer. NOAA OCSEAP Final Rep. No. 63. pp. 63–121.

Fechhelm, R.G., Dillinger, R.E., Gallaway, B.J., and Griffiths, W.B. 1992. Modeling of in situ temperature and growth relationships for yearling broad whitefish in Prudhoe Bay, Alaska. Trans. Am. Fish. Soc. **121**: 1–12.

Fechhelm, R.G., Griffiths, W.B., Bryan, J.D., Gallaway, B.J., and Wilson, W.J. 1995. Application of an in situ growth model: inferred instance of interspecific trophic competition between amphidromous fishes of Prudhoe Bay, Alaska. Trans. Am. Fish. Soc. **124**: 55–69.

Furniss, R.A. 1975. Inventory and cataloging of arctic area waters. Alaska Dep. Fish Game Annu. Rep. Fed. Aid Fish Res. Sport Fish Div. **16**: 1–45.

Glova, G., and McCart, P. 1974. Life history of Arctic char (*Salvelinus alpinus*) in the Firth River, Yukon Territory. Arctic Gas Biol. Rep. Ser. 40.

Golikov, A.N., and Averincev, B.G. 1977. Distribution patterns of benthic and ice biocenes in the high latitudes of the polar basin and their part in the biological structure of the world oceans. Polar oceans. Proceedings of the Polar Oceans Conference, May 1975. *Edited by* M. Dunbar. Arctic Institute of North America, Calgary, Alta. pp. 331–364.

Griffiths, W.B, and Dillinger, R.E. 1981. Invertebrates. *In* Environmental assessment of the Alaskan continental shelf. Vol. 8, Part 5. NOAA Outer Continental Shelf Environ. Assess. Program Final Rep. Prin. Inv.

Griffiths, W.B., Gallaway, B.J., Gazey, W.J., and Dillinger, R.E. Jr. 1992. Growth and condition of Arctic cisco and broad whitefish as indicators of casueway-induced effects in the Prudhoe Bay region, Alaska. Trans. Am. Fish. Soc. **121**: 1–21.

Knutzen, J.A., and Jewett, S.C. 1991*a*. Fish food habits (stomachs). Vol. 6, Chap. 2. *In* 1987 Endicott Environmental Monitoring Program. Report by Envirosphere Company to U.S. Army Corps of Engineers, Alaska District, Anchorage, Alaska. (Available from Envirosphere Company, 10900 8th St., Bellevue, WA 98004-4405.)

Knutzen, J.A., and Jewett, S.C. 1991*b*. Fish prey surveys (drop nets). Vol. 6, Chap. 3. *In* 1987 Endicott Environmental Monitoring Program. Report by Envirosphere Company to U.S. Army Corps of Engineers, Alaska District, Anchorage, Alaska. (Available from Envirosphere Company, 10900 8th St., Bellevue, WA 98004-4405.)

Knutzen, J.A., Brancato, M.S., and Jewett, S.C. 1990*a*. Fish food habits (stomachs). Vol. 7, Chap. 2. *In* 1986 Endicott Environmental Monitoring Program. Report by Envirosphere Company to U.S. Army Corps of Engineers, Alaska District, Anchorage, Alaska. (Available from Envirosphere Company, 10900 8th St., Bellevue, WA 98004-4405.)

Knutzen, J.A., Brancato, M.S., and Jewett, S.C. 1990*b*. Fish prey surveys (drop nets). Vol. 7, Chap. 3. *In* 1986 Endicott Environmental Monitoring Program. Report by Envirosphere Company to U.S. Army Corps of Engineers, Alaska District, Anchorage, Alaska. (Available from Envirosphere Company, 10900 8th St., Bellevue, WA 98004-4405.)

LGL (Alaska Research Associates, Inc.) 1990. Recruitment and population studies, analysis of 1988 fyke net data. Vol. II. *In* The 1988 Endicott Development Fish Monitoring Program. Report by LGL Alaska Research Associates, Inc. for BP Exploration (Alaska) Inc., Anchorage, and North Slope Borough, Anchorage, Alaska. (Available from LGL Alaska Research Associates, Inc., 4175 Tudor Centre Dr., Anchorage, AK 99508.)

McCart, P., and Craig, P. 1971. Meristic differences between anadromous and freshwater-resident Arctic char (*Salvelinus alpinus*) in the Sagavanirktok River drainage, Alaska. J. Fish. Res. Board Can. **28**: 115–118.

Morrow, J.E. 1980. The freshwater fishes of Alaska. Alaska Northwest Publ. Co., Anchorage, Alaska.

Moulton, L., Gallaway, B., Fawcett, M., Griffiths, W., Critchlow, K., Fechhelm, R., Schmidt, D., and Baker, J. 1986. 1984 Central Beaufort Sea fish study. Vol. 2, Chap. 3. *In* Prudhoe Bay Waterflood Project Environmental Monitoring Program 1984. Report by Woodward-Clyde Consultants, Entrix, Inc. and LGL Ecological Research Associates, Inc. to Envirosphere Company, Bellevue, Wash., and U.S. Army Corps of Engineers, Anchorage, Alaska. (Available from Envirosphere Company, 10900 8th St., Bellevue, WA 98004-4405.)

Neter, J., Wasserman, W., and Kutner, M.H. 1989. Applied linear regression models. Irwin, Boston, Mass.

Niedoroda, A.N, and Colonell, J.M. 1990. Beaufort Sea causeways and coastal ocean dynamics. *In* 19th Proceedings of the 8th Offshore Mechanical and Engineering Conference. American Society of Engineers, New York. pp. 203–218.

Schrader, C.G, and Hachmeister, L.E. 1990. Ice breakup/freezeup. Vol. 7, Part III, Chap. 3. *In* 1986 Endicott Environmental Monitoring Program. Report by Envirosphere Company to U.S. Army Corps of Engineers, Alaska District, Anchorage, Alaska. (Available from Envirosphere Company, 10900 8th St., Bellevue, WA 98004-4405.)

Stringer, W.J. 1987. Ice breakup/freezeup. Vol. 5, Chap. 1. *In* 1985 Endicott Environmental Monitoring Program. Report by Envirosphere Company to U.S. Army Corps of Engineers, Alaska District, Anchorage, Alaska. (Available from Envirosphere Company, 10900 8th St., Bellevue, WA 98004-4405.)

Thorsteinson, L.K., Jarvela, L.E., and Hale, D.A. 1990. Arctic fish habitat investigations: nearshore studies in the Alaskan Beaufort Sea, summer 1988. NOAA Outer Continental Shelf Environ. Assess. Program Final Rep. No. 71. pp. 349–485.

Underwood, T.J., Gordon, J.A., Thorpe, L.A., Millard, M.J., and Osborne, B.M. 1995. Characteristics of selected fish populations of Arctic National Wildlife Refuge coastal waters, final report, 1988–1991. Report of the Fisheries Research Office, U.S. Fish and Wildlife Service, Fairbanks, Alaska.

Walters, V. 1955. Fishes of western arctic America and eastern arctic Siberia. Taxonomy and zoogeography. Bull. Am. Mus. Nat. Hist. **106**: 259–368.

Wilkinson, L. 1989. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Ill.

Yoshihara, H.T. 1972. Monitoring and evaluation of arctic waters with emphasis on the North Slope drainages. Alaska Dep. Fish Game Annu. Rep.

Scale-dependent variations in the precision of larval fish abundance estimates: a study of *Sebastes* sp. on Flemish Cap

P. Pepin and J.T. Anderson

Abstract: We test the assumptions of synopticity over a 6-d sampling period and homogeneity within a 40 × 40 km stratum by investigating the effect of sampling scale, or station spacing, on the precision (i.e., variance) of abundance estimates of larval redfish (*Sebastes* sp.). We contrast the results obtained for larval redfish with observations of scale-dependent variability in temperature, salinity, chlorophyll, and zooplankton, which have been shown to be interrelated in other systems. In contrast with previous studies, our results show that the patterns of variance in temperature, salinity, chlorophyll, and zooplankton are not scale dependent. Although the assumption of synopticity cannot be rejected, our results show that the variance in abundance of larval redfish is scale dependent and that it is much greater than the variances of the other variables considered. The contrasting pattern may be due to differences in the relative importance of physical and biological processes during the very early life history of marine fish. We suggest that sampling programs must be preceded by pilot studies designed to determine the effort required to obtain the most precise estimates of abundance given the limitations caused by the underlying sampling variability and the influence of physical processes.

Résumé : Nous avons testé les hypothèses de synopticité au cours d'une période d'échantillonnage de 6 jours et d'homogénéité à l'intérieur d'une strate de 40 × 40 km en étudiant l'effet de l'échelle d'échantillonnage, ou de l'espacement des stations, sur la précision (c.-à-d. la variance) des valeurs estimées de l'abondance du sébaste (*Sebastes* sp.) larvaire. Nous avons comparé les résultats obtenus pour le sébaste larvaire avec les observations de la variabilité dépendante de l'échelle touchant la température, la salinité, la chlorophylle et le zooplancton, facteurs qui, dans d'autres systèmes, se sont révélés interdépendants. Contrairement aux études antérieures, nos résultats montrent que les profils de variance touchant la température, la salinité, la chlorophylle et le zooplancton ne dépendent pas de l'échelle. Bien que l'hypothèse de synopticité ne puisse être rejetée, nos résultats montrent que la variance de l'abondance du sébaste larvaire dépend de l'échelle et qu'elle est beaucoup plus grande que celle des autres variables prises en considération. La divergence observée peut être attribuable à des différences touchant l'importance relative des processus physiques et biologiques survenant durant les tout premiers stades du cycle vital des poissons marins. Nous estimons que les programmes d'échantillonnage soient précédés d'études pilotes visant à déterminer l'effort nécessaire pour obtenir l'estimation la plus précise de l'abondance étant donné les limites imposées par la variabilité d'échantillonnage sous-jacente et l'effet des processus physiques.
[Traduit par la Rédaction]

Introduction

Variations in the survival of ichthyoplankton may be the result of short-term catastrophic losses during a particularly sensitive life history stage (e.g., Hjort 1914), or they may be the result of more subtle changes in either mortality or growth rates accumulated over extended periods (e.g., Smith 1985; Houde 1987; Beyer 1989). Failure to observe the widespread occurrence of catastrophic events during the egg or larval stages of fish development (e.g., O'Connell 1980; Hewitt et al. 1985; Mullin et al. 1985; McGurk 1989) indicates that more subtle changes in vital rates may be determining variations in survival. If correct, detecting slight variations in mortality rates may be difficult to achieve because of the low precision often associated with estimates of ichthyoplankton abundance (Smith and Richardson 1977; Lo 1985, 1986; Cyr et al. 1992). It has been argued that ichthyoplankton studies are often conducted on space and time scales that are inappropriate for the study of patchily distributed organisms with high turnover rates (i.e., development and (or) loss) (Leggett 1986; Anonymous 1992; Pepin 1993).

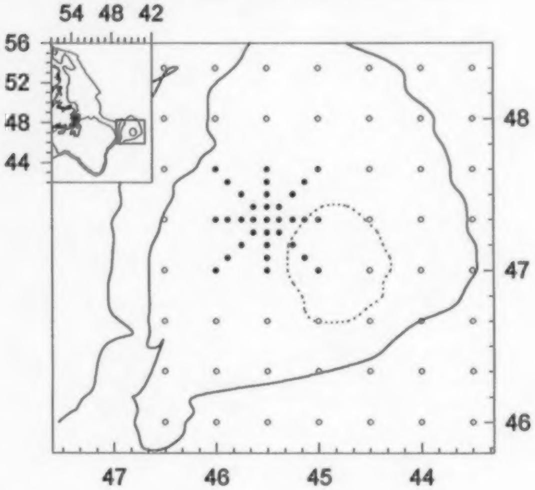
Ichthyoplankton surveys are designed to take quasi-synoptic samples of a population. Most often, the sampling design consists of a grid of stations that covers the geographical range of the population (Cassie 1968; Smith and Richardson 1977). Systematic sampling assumes that the first station is located at the center within the stratum defined by the sampling grid (Cassie 1968; Cochran 1977). This approach is precise if one assumes homogeneity of variance within strata and heterogeneity among strata (i.e., that the correlation between strata is approximately zero), that all samples taken during a single cruise are synoptic, and that the geographic range of a population is sampled (Cochran 1977; Smith and Richardson 1977). However, these assumptions are seldom tested.

The importance and magnitude of sampling variability in the study of aquatic organisms are well recognized (Elliot 1973; Downing et al. 1987; Cyr et al. 1992). In the study of ichthyoplankton populations, sampling designs often represent a compromise between high-frequency sampling of a small population or patch (e.g., Talbot 1977; Fortier and Leggett

Received January 4, 1995. Accepted October 7, 1996.
J12698

P. Pepin and J.T. Anderson. Department of Fisheries and Oceans, P.O. Box 5667, St. John's, NF A1C 5X1, Canada.

Fig. 1. Map of survey grid showing the nested design (solid circles) and broad-scale survey (open circles). Dotted and solid lines represent the 200- and 1000-m isobaths, respectively.



1985; Munk et al. 1986; Heath and MacLachlan 1987) or the low-frequency sampling of a population's range using relatively wide station separation (e.g., 40 km) (e.g., Zweifel and Smith 1981; Morse 1989). Relatively little is known about the most appropriate scale that should be used for the study of ichthyoplankton populations, but there is a growing basis of information from which we can draw inferences. The aggregation of information from a variety of sources (e.g., Downing et al. 1987; Cyr et al. 1992) and the availability of particle counters and acoustic measurements of animal abundance (e.g., Mackas and Boyd 1979; Mackas et al. 1985; Tsuda et al. 1993) provide a basis for the understanding and prediction of sampling variability. First, replicate sampling of planktonic organisms clearly shows that the variance among samples increases as the mean abundance of animals increases, generally following a power law (i.e., $s^2 = ax^b$, where s^2 is the variance, x is the mean abundance of animals, a is a constant, and b is the exponent) with an exponent ranging from 1.5 to 1.85 (Downing et al. 1987; Pinel-Alloul et al. 1988; Cyr et al. 1992). Such a relationship suggests that as animals become more abundant, the coefficient of variation for estimates of abundance decreases. Second, there is a strong body of evidence to suggest that the spatial scale of variability in the abundance of organisms varies among different types of organisms. Variability in the abundance of organisms at lower trophic levels, such as phytoplankton, appears to closely match the spatial variability of physical variables, such as temperature and salinity (e.g., Platt and Denman 1975; Mackas and Boyd 1979; Weber et al. 1986; Tsuda et al. 1993). Spectral representation of the variance along a transect indicates that much of the variability occurs over large spatial scales, often referred to as a "red spectrum". Larger organisms, such as copepods, appear to be less closely tied to variations in the physical environment (Mackas and Boyd 1979; Weber et al. 1986; Tsuda et al. 1993), showing a distribution pattern that is characterized as a "white noise spectrum". The heterogenous distribution of such organisms led Weber et al. (1986) to suggest that the precision of population estimates would be largely independent of the scale at which surveys were designed beyond the typical dimension of a patch (i.e., 1–2 km). If such conclusions can be found to apply to ichthyoplankton, survey designs that maximize stratum size or station separation would be more appropriate (Weber et al. 1986; Tsuda et al. 1993).

This study presents the results of a series of surveys of redfish (*Sebastes* sp.) larvae conducted on Flemish Cap (47°N, 45°W). Early work on Flemish Cap had indicated that a single ship sampling at stations spaced 40 km apart over a 6- to 7-d period would meet the survey assumptions of homogeneity within strata and synopticity (Anonymous 1978). Results for both fish larvae (Anderson 1984) and invertebrate zooplankton (Anderson 1990) had indicated that populations were contained within a 56-station grid. Our objectives here were to test the assumptions of homogeneity within strata and synopticity within a sampling cruise by investigating the effect of sampling scale, or station spacing, on the precision (i.e., variance) of larval fish population estimates. We contrast the results obtained for larval redfish with observations of the scale-dependent variability in temperature, salinity, chlorophyll concentration, and zooplankton abundance, all of which have been shown to be interrelated in other systems (Mackas and Boyd 1979; Weber et al. 1986; Tsuda et al. 1993). The study was part of a large-scale study of the Flemish Cap region designed to estimate variations in growth and survival of redfish larvae (Anderson 1984).

Materials and methods

Study area

Flemish Cap is a bank approximately 300 nautical miles east of Newfoundland and is isolated from the Grand Banks by a pass 1000 m deep. The top of the bank is relatively flat, ranging from 125 to 300 m in depth. Two major oceanic currents surround Flemish Cap: the cold, low-salinity Labrador current on the western and northern sides of the Cap and the relatively warm, high-salinity Gulf Stream on the southern flank. A weak anticyclonic gyre overlies the top of the bank (Ross 1980).

Survey design

The study was designed to estimate the mean and variance in the abundance of larval *Sebastes* sp. based on samples from a grid of nine stations separated by fixed distances (10, 20, 30, 40, or 80 km). For each grid scale, overall mean and variance were estimated based on a total sample size of nine stations (see below). The protocol was developed to eliminate the potential effect of differing sample numbers on the precision of each estimate. Our study was conducted using two surveys.

The first survey consisted of a nested grid design developed to determine variations in abundance estimates on grid scales of 10, 20, 30, and 40 km. Two ships sampled stations located at intervals of 10 km of latitude and (or) longitude along four intersecting transects: one oriented along a north–south axis, one along an east–west axis, and two diagonals along north–south/east–west axes (Fig. 1). The result of this sampling scheme was to produce four sampling grids of nine stations, centered on a common point, and separated by 10, 20, 30, and 40 km from the adjacent stations on each grid. The grid of nine stations separated by 40 km corresponds to a sample of strata around each station typical of the large-scale survey of the region (Anderson 1984) in which station separation was 40 km. This nested survey was repeated three times over a 6-d period (30 June – 5 July 1981). The center station was occupied four times during each pass of the grid. Only the first occupation of the station was used in estimating the sample mean and variance for each grid scale. The four repeated occupations of the center station were used to estimate abundance and sampling variability at a single location. This approach is similar to that of Greig-Smith (1952) who investigated the effect of quadrat size on sampling variability.

The second set of surveys was designed to sample the entire population of larval *Sebastes* sp. in the Flemish Cap region (see Anderson 1984). During 1981, three complete regional surveys were conducted along a grid with each station separated by 40 km in latitude and (or) longitude from the nearest station(s). These surveys, typical of the large-scale sampling pattern for the study area (Anderson 1984), were carried out during 2–9 May, 22–27 May, and 22–30 June 1981. From these surveys, we were able to estimate the variance in abundance estimates for station separations of 40 and 80 km. The mean and variance in abundance estimates were determined by a repeated subsampling of the grid. Each station along the grid was selected as the center point of a group of nine stations, distant by 40 or 80 km in latitude, longitude, or both. For each selected set of stations, we calculated sample mean and variance. Stations at the boundary of the survey grid could not be used as the center point of a sample set because the total number of observations for each estimate of abundance was less than nine.

Sampling protocol

In both the nested and regional surveys, plankton samples were obtained at each station using 61-cm bongo nets towed at 3 knots ($1.5\ \mathrm{m \cdot s^{-1}}$). Single oblique tows to 200 m were conducted with payout and retrieval rates of 0.83 and $0.33\ \mathrm{m \cdot s^{-1}}$. Each net was made of 0.333-mm nitex and fitted with a General Oceanics flowmeter. Samples were preserved in 5% buffered formaldehyde. All ichthyoplankton were sorted from each paired sample and identified to the lowest taxonomic level possible. An abundance estimate at each station was calculated as

$$N = \frac{CD}{\pi r^2 L}$$

where N is the number of redfish larvae per square metre, C is the number of larvae collected (n), D is the maximum sample depth (metres), L is the distance towed (metres), and r is the radius of the net opening (metres). In addition, zooplankton displacement volume (millilitres per square metre) was measured at all stations during each pass of the nested survey.

During the first pass of the nested survey, temperature, salinity, and chlorophyll concentrations were measured. Oceanographic observations were collected using a Guildline Mark IV CTD fitted to a rosette sampler. Water samples were taken at the surface, 10, 20, 30, 50, 75, and 125 m to obtain measurements of chlorophyll which was extracted according to procedures outlined by Strickland and Parsons (1968). In the following analysis, each depth stratum was used as an independent observation.

Analysis

For all combinations of nine adjacent (nearest-neighbour) stations, at a fixed scale of latitudinal/longitudinal separation, we calculated sample mean ($\bar{x} = n^{-1} \sum x$, where x is the sample observation and n is the number of observations) and variance ($s^2 = (n-1)^{-1} \sum (x - \bar{x})^2$) for each variable measured (ichthyoplankton, zooplankton, chlorophyll, temperature, and salinity). Geometric mean and variance were not used in our analysis because of the potential bias and loss of efficiency when data do not follow a lognormal distribution but follow other types of skewed distributions (e.g., negative binomial) (Myers and Pepin 1990, 1991).

Because of the power relationship ($s^2 = a\bar{x}^b$) between replicate sample mean and variance found for biological variables (Downing et al. 1987; Pinel-Alloul et al. 1988; Cyr et al. 1992), we chose to assess the effect of grid scale on the precision of population estimates for ichthyoplankton, zooplankton, and chlorophyll using an analysis of covariance (ANCOVA). After log-transformation of the sample mean and variance, we estimated the effect of grid scale, measured as a classification variable, as

$$Y_i = \mu + \alpha_i + \beta X + \varepsilon$$

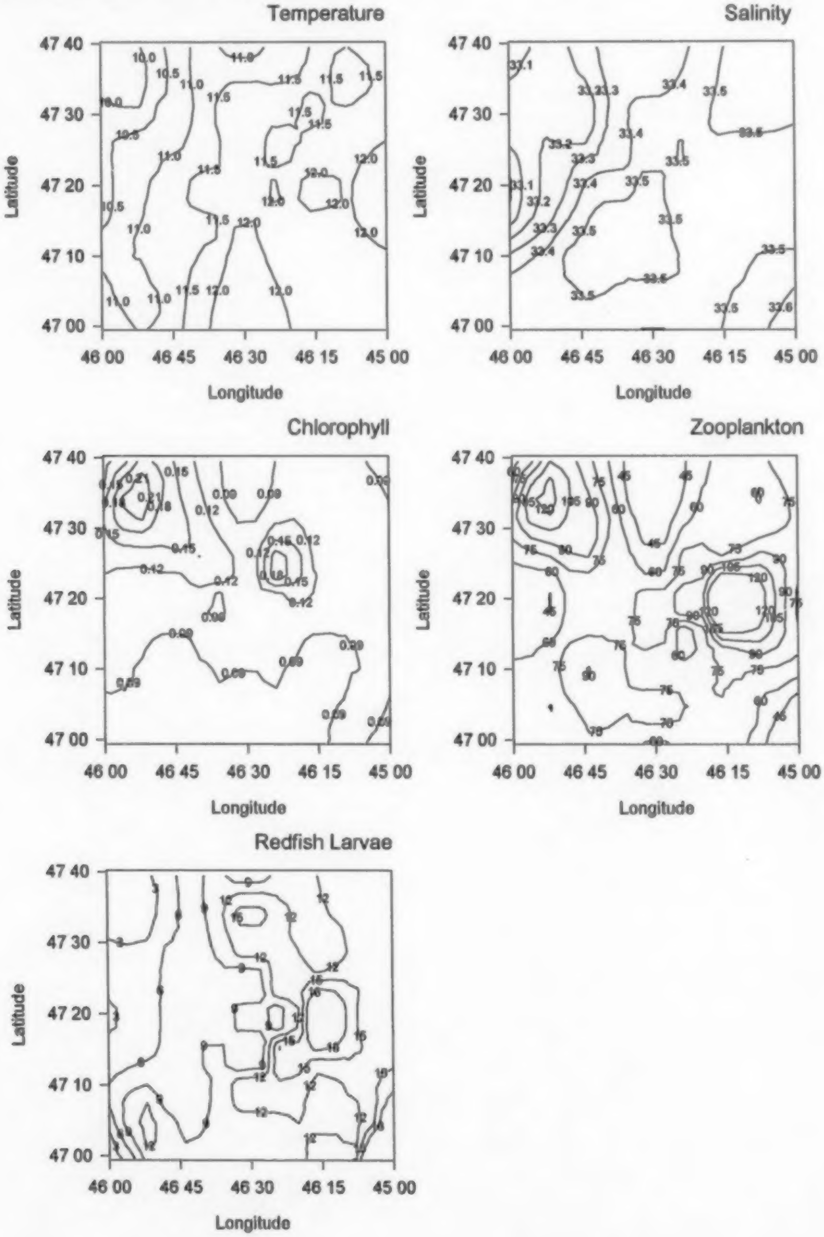
where Y_i is the log-transformed population variance ($\log_{10} s^2$), μ is the grand mean, α_i is the classification (i.e., treatment) effect for each grid scale i, β is the slope of the relationship, X is the log-transformed estimate of the population mean ($\log_{10} \bar{x}$), and ε is the error. The classification variables represented each grid scale from the nested surveys (10, 20, 30, and 40 km for all variables) and the grid scales for the combined data from the three large-scale surveys (40 and 80 km for redfish larvae only). Our approach consisted of first assessing the equality of slopes among classification variables (i.e., grid scales), followed by an assessment of the coincidence among treatments (i.e., equality of intercepts given equality of slopes). The least squares estimates of grid scale marginal estimate of the variance for each independent observation (i.e., survey and grid scale) were calculated as the fixed treatment effect given that the covariate (i.e., log-transformed estimate of the population mean) was held at the overall mean. When there is no relationship between sample mean and variance, the model reduces to an analysis of variance (ANOVA) among grid scales. The approach taken in our study is similar to that taken by Downing (1991) and Pinel-Alloul and Pont (1991), although we test for equality in slopes among treatments rather than restrict ourselves to a comparison of the residuals from a common variance-to-mean relationship. We did ensure that there was appropriate overlap in the data from the different grid scales, as indicated by Downing (1991).

Results

Measurements of sea surface temperature and salinity taken during the first pass over the nested grid showed a notable gradient along the east–west axis (Fig. 2). This may reflect a difference between water overlying Flemish Cap and that of the Labrador current flowing through Flemish Pass, located between Flemish Cap and the Grand Banks (Akenhead 1986). The cross-isobath gradient in physical characteristics was not reflected in either the distribution of surface chlorophyll concentration or zooplankton displacement volume (Fig. 2). Both phytoplankton and zooplankton appear to be patchily distributed within the area of the nested grid, but their distribution is largely uncorrelated with the surface distribution of temperature, salinity, or between themselves (Table 1). The distribution of redfish larvae showed a gradient along the same axis similar to that exhibited by both temperature and salinity (Fig. 2) and was significantly correlated with these variables but was not correlated with the abundance of phytoplankton or zooplankton (Table 1). During each of the three passes over the nested grid, the concentration of redfish was highest in the southeasterly corner of the grid and lowest in the northwesterly corner. Although there are differences in the distribution pattern among the three passes, the center of mass of the larval redfish population showed a maximum displacement of 7 km in a southeasterly direction between surveys.

Although there was evidence of an increase in estimated variance with increasing separation between stations (Fig. 3), the effect of increasing grid scale was only significant in the case of larval redfish (Table 2). There is a substantial increase in the adjusted mean variance as the separation between stations increases from 30 to 40 km (Fig. 3). With the exception of temperature, the estimated variance in the various oceanographic variables was significantly related to the mean, although there was no indication of variations in the slope of the

Fig. 2. Contour diagram of temperature (°C), salinity (ppt), chlorophyll concentration ($\mu g \cdot L^{-1}$), zooplankton displacement volume ($mL \cdot m^{-2}$), and redfish larvae (no.$\cdot m^{-2}$) observed during the first pass of the nested grid. Contours were determined using a combination of Laplacian and spline interpolation schemes (Young and van Woert 1991).



relationships among grid scales (Table 2). Variance in salinity decreased with increasing mean ($\beta_{sal} = -0.029$), reflecting increasing stability with increasing depth. In the case of chlorophyll, zooplankton displacement, and larval redfish abundance, the estimated variance increased with increasing mean ($\beta_{chl} = 2.25$, $\beta_{zplk} = 2.40$, $\beta_{lar} = 1.85$) (Fig. 4).

Mean abundance of redfish larvae within the nested sampling grids showed a consistent pattern of decreasing abundance among the different sampling periods, with the exception of the largest grid scale which was due to a single large observation in the southwestern-most corner during the second pass (Fig. 5). Variance estimates were homogenous among grid scales ($F_{3,104} = 1.90$, $p > 0.1$) as were variance estimates among the different sampling periods ($F_{2,105} = 1.28$, $p > 0.2$). An ANOVA on the pooled samples from each pass revealed that there were no significant differents in mean abundance

Table 1. Spearman rank correlation coefficient, and associated probability below (italicized), among the oceanographic variables measured during the nested survey of Flemish Cap.

Variable	Salinity	Chlorophyll	Zooplankton	Redfish
Temperature	0.25	−0.20	0.16	0.30
	0.04	*0.12*	*0.20*	*0.01*
Salinity		−0.10	−0.01	0.27
		0.45	*0.94*	*0.03*
Chlorophyll			0.15	−0.09
			0.25	*0.49*
Zooplankton				−0.03
				0.83

over the 6-d period ($F_{2,105} = 1.17$, $p > 0.3$). However, when only the end points (passes 1 and 3) are considered, the comparison suggests a marginal difference in mean abundances ($t = 1.76$, $0.1 > p > 0.05$) which yielded an estimated mortality rate of $0.055 \cdot d^{-1}$.

Discussion

The results for redfish indicate that surveys conducted over a 6-d sampling period in this region may be considered synoptic. Furthermore, the results clearly show that the assumption of homogeneity of variance within strata for the regional survey (i.e., the nested grid with 20-km station spacing, corresponding to stratum dimension for a regional station separation of 40 km) is valid. The assumption of homogeneity would be violated if stratum size exceeded 30 km on either side of the center point of a nested grid (i.e., 60-km station spacing in a regional survey). Ichthyoplankton in our study exhibit a statistically significant difference in estimated variance at a nested grid scale between 30 and 40 km. The estimated variance in abundance is substantially lower for a nested grid scale of 30 km or less, although there is a continued decrease in variability as the grid scale becomes finer.

Synopticity of a 6-d survey for the area of Flemish Cap is due partly to the characteristics of the organism under study. Anderson (1984) estimated average losses of approximately $5\% \cdot d^{-1}$ from the redfish population on Flemish Cap, close to that estimated using nested survey passes 1 and 3. Given that the coefficient of variation in the pooled sample mean abundance measured during the nested surveys is approximately 15%, a mortality rate of approximately $7–8\% \cdot d^{-1}$ would have been required to yield a significant difference in abundances between surveys conducted 5 d apart. However, we should note that our results using only the two end points (passes 1 and 3) were nearly significant. Under circumstances where mortality rates would have been greater, significant changes in abundance within the survey area could have occurred during the typical sampling period used during regional surveys. Such losses during a survey can add substantial variation to estimates of abundance because not only is the number of animals decreasing through time but the relative variability in sampling precision is also decreasing because of the strong variance-to-mean relationship (Cyr et al. 1992; this study).

The combined effect of sampling variability and a lack of synopticity in a survey can be illustrated using a simple model with different mortality scenarios (details of the calculations are in the legend to Fig. 6). For the case of a uniformly distributed population within random sampling variability, calculations show that the estimated mean abundance becomes increasingly greater than the actual number of animals as the duration of a survey is increased (Fig. 6). When sampling variability is added to the variance in estimated daily mean abundance, the precision of the overall estimate of abundance decreases substantially (Fig. 6). As the mortality rate of the population increases, the effect of sampling synopticity becomes more important. Although our model does not consider the effect of sample number on the quality of the estimates of abundance and the power to differentiate means from two surveys (e.g., Cyr et al. 1992), the potential importance of ensuring that surveys provide a synoptic sample of ichthyoplankton populations is evident. Unless surveys are designed to ensure quasi-synoptic coverage, variations in mortality rates could be difficult to detect.

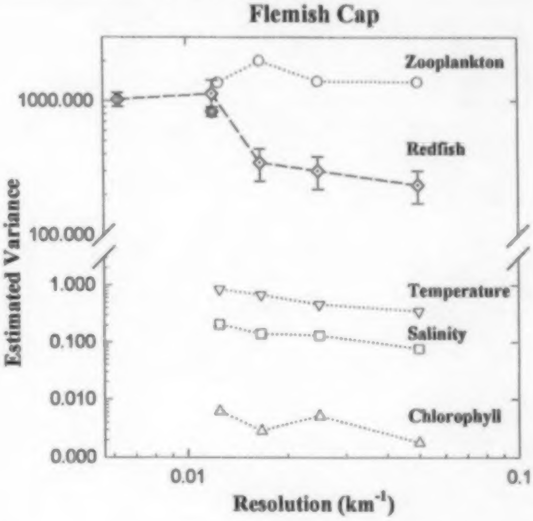


Fig. 3. Estimated variance in temperature, salinity, chlorophyll concentration, zooplankton displacement volume, and *Sebastes* sp. larvae in relation to resolution (1/[distance between stations]). The data for salinity, chlorophyll, and zooplankton are the marginal variance estimates from the ANCOVA which included the relationship between sample mean and variance. The data for larval *Sebastes* sp. are marginal variance estimates from the ANCOVA which included the relationship between sample mean and variance for the nested (open diamonds) and regional surveys (shaded diamonds). Error bars represent the standard error in estimated variance determined by ANCOVA.

The strong scale-dependent pattern in the variance in abundance of larval redfish differs from that observed for some copepods (Tsuda et al. 1993) and krill (Weber et al. 1986) for which the typical patch size appears to be substantially less than any reasonable station separation (i.e., of the order of less than 1–2 km). In addition, ichthyoplankton from this study show scale dependency in the variance in abundance whereas other oceanographic parameters (i.e., temperature, salinity, chlorophyll, zooplankton displacement volume) do not, which is in contrast with observations by Weber et al. (1986). However, the results from this study are consistent with observations by Frank et al. (1993) that contrast the broad-scale

Table 2. Results of the ANCOVA, using the log-transformed mean and variance, for each oceanographic variable.

Variable	Source	df	Type I SS	*F*-value	Significance	Type III SS	*F*-value	Significance
Temperature	Grid scale	3	0.87	0.73	>0.5	1.10	0.98	>0.5
	Mean	1	0.30	0.75	>0.4	0.30	0.80	>0.3
	Interaction	1	0.11	0.28	>0.6			
	Error	13	4.78					
Salinity	Grid scale	3	0.00024	0.66	>0.5	0.0005 7	1.55	>0.2
	Mean	1	0.0014	11.8	<0.001	0.0014	11.9	<0.001
	Interaction	1	0.00011	0.89	>0.3			
	Error	12	0.0015					
Chlorophyll	Grid scale	3	0.70	0.62	>0.6	0.32	0.31	>0.8
	Mean	1	15.0	40.3	<0.001	15.0	43.6	<0.001
	Interaction	1	0.01	0.02	>0.9			
	Error	12	4.48					
Zooplankton	Grid scale	3	0.079	1.11	>0.5	0.056	1.19	>0.3
	Mean	1	0.26	10.9	<0.05	0.26	16.5	<0.01
	Interaction	3	0.015	0.20	>0.8			
	Error	4	0.096					
Redfish larvae	Grid scale	5	1.71	6.78	<0.001	1.71	6.73	<0.001
	Mean	1	94.1	1870	<0.001	37.3	735	<0.001
	Interaction	5	0.28	1.11	>0.3			
	Error	73	3.67					

Note: Type III sums of squares, and corresponding *F*-values, were computed after removing the nonsignificant interaction term from the analysis for each taxa. Type III sums of squares represent partial sums of squares obtained when each independent variable is the last added to the model. The error sum of squares was estimated as the total of the Type I sums of squares for both error and interaction terms.

patchiness of larval capelin (*Mallotus villosus*) with that of chaetognaths (*Sagitta elegans*) on the Grand Banks. Frank et al. (1993) showed that larvae exhibited inherently greater spatial heterogeneity, throughout all early life history stages, than other zooplankters. Unlike other macrozooplankton, it appears that the choice of grid resolution may influence the precision of population estimates of ichthyoplankton. These results suggest that ichthyoplankton populations may exhibit two scales of distribution, one reflecting the patchiness within aggregations and the other reflecting the separation between aggregations or large-scale distribution patterns. Such a pattern may arise as the relative importance of biological and physical processes changes throughout the early life history.

The slope of the variance-to-mean relationship estimated for larval redfish is within the range of previous observations by Downing et al. (1987), Pinel-Alloul et al. (1988), Pace et al. (1991), Pinel-Alloul and Pont (1991), Cyr et al. (1992), and P. Pepin and T.H. Shears (unpublished data). This is consistent with the demographic model of spatial distribution with moderate environmental heterogeneity, which predicts that values of β will rarely lie outside the range of 1–2 (Anderson et al. 1982; Downing 1986, 1991), at least within the confines of individual strata. Anderson (1984) noted that spawning of redfish occurs primarily along the edges of Flemish Cap, following which larvae disperse primarily onto the Cap. During the early life stages of development, the weak gyral circulation in the area (Ross 1980) appears to have a significant influence on the distribution of larvae, as suggested by their association with the temperature and salinity distribution. Smith (1973) and Hewitt (1981) studied variations in the distribution of the early life history stages of Pacific sardine (*Sardinops caerulea*) and northern anchovy (*Engraulis mordax*), respectively. They both observed that eggs and larvae were initially patchily distributed and that physical dispersion and coalescence of patches resulted in a progressively more uniform distribution. This process continues until a stage where predator–prey interaction coupled with behavioural cues can lead to increased aggregation, and hence variance in population abundance (Hewitt 1981). The distribution pattern observed during our broad-scale survey in June of 1981, immediately preceding our nested survey, was the most widely dispersed (i.e., the lowest variance among samples in the broad-scale survey) for the three surveys of that year (after correcting for differences in mean abundance), indicating that reaggregation into schools was minimal (Anderson 1984). Spawning distributions and transport may play a relatively greater role during early development of ichthyoplankton distributions whereas biological interactions (e.g., behaviour, prey–predator interactions) may become more important later in development. As a result, the sampling design required to address biological interactions may have different requirements than one dealing with the influence of transport on distribution patterns (Frank 1988; Frank and Leggett 1985; P. Pepin and Helbig, unpublished data).

Legendre and Demers (1984) suggested that in order to prevent aliasing of temporal trends in measurements of abundance or processes, survey strategies should ensure that sampling be conducted on a time scale that is at least half of the highest frequency of fluctuations. The same is applicable to the spatial sampling scale of ichthyoplankton. Cochran (1977) stated that knowledge of the population structure is necessary for the most effective use of a systematic survey design. Instances where there is a linear or periodic pattern in population distribution can lead to bias and loss of efficiency in population estimates. We have presented evidence that suggests that station separations exceeding 40–60 km on Flemish Cap may undersample the population and thus may lead to an inaccurate representation of abundance. We do not conclude that a regional

Fig. 4. Estimated variances in chlorophyll concentration ($\log_{10}s^2 = 0.24 + 2.26 \log_{10}\bar{x}$, $r^2 = 0.78$), zooplankton displacement volume $\log_{10}s^2 = -1.46 + 2.40 \log_{10}\bar{x}$, $r^2 = 0.76$), and population abundance of larval *Sebastes* sp. ($\log_{10}s^2 = 0.23 - \alpha_i + 1.85 \log_{10}\bar{x}$, $r^2 = 0.96$, where $\alpha_i = -0.55$ for sampling scales <40 km and $\alpha_i = -0.02$ for sampling scales ≥40 km), based on samples from nine stations, in relation to the mean abundance.

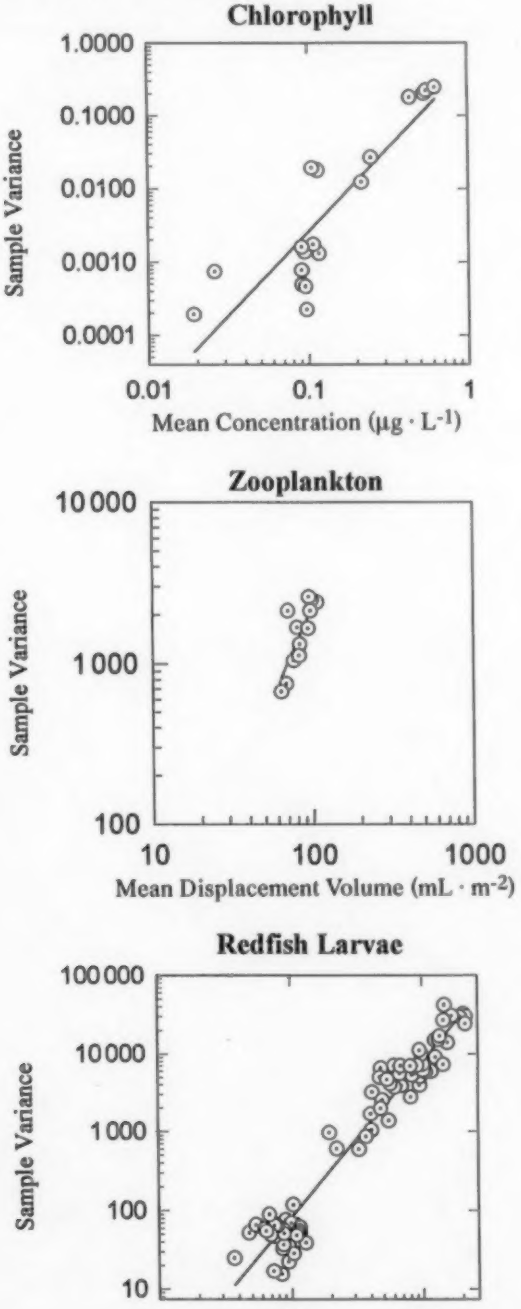
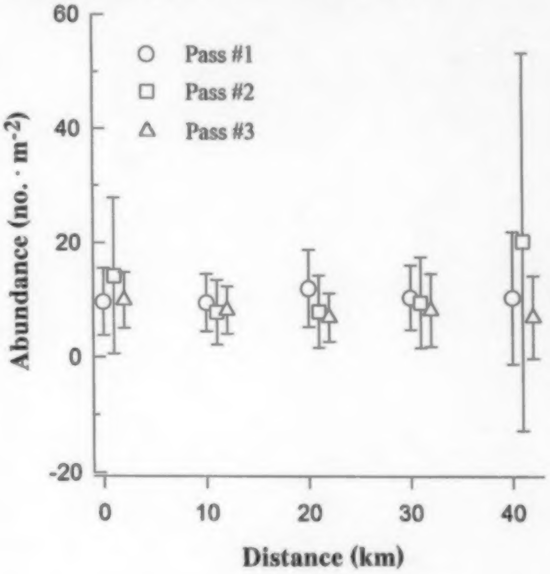


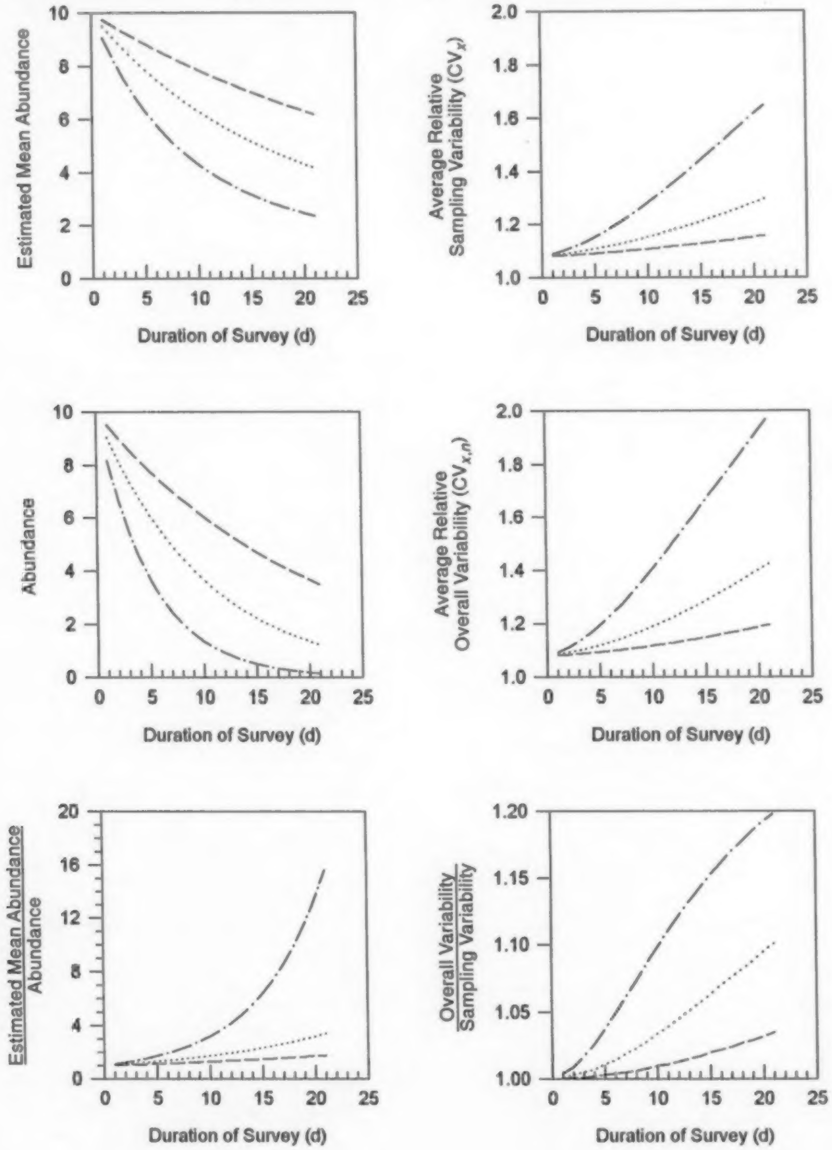
Fig. 5. Mean abundance (± 1 SD) of *Sebastes* sp. larvae sampled on Flemish Cap during three complete passes of the nested grid. The estimated mean, and standard deviations, for the 0-km scale is based on the data from the four occupations of the central station during each pass of the nested survey grid. Data for each pass are offset by 1 km along the *x*-axis to facilitate viewing.



station separation of approximately 40 km is an appropriate sampling scale for all ichthyoplankton studies. Whether the distinct scale-dependent pattern in estimated variance would be found for other species and systems is unknown. Flemish Cap is characterized by a particularly weak gyral circulation and there is no evidence of a strong frontal definition, as found on a number of other banks (Loder et al. 1988). Oceanographic conditions in other regions will have an impact on the distribution and dispersal of ichthyoplankton species in these particular systems. Although physical processes clearly influence planktonic organisms, we must keep in mind that biological production and loss will also contribute to the distribution of fish eggs and larvae. The complexity of possible interactions among biological and physical processes highlights the need to empirically determine the most appropriate survey scale for individual systems. We feel that this need is particularly important because one of the fundamental issues many have tried to address involves the link between early life history events and subsequent recruitment (Hjort 1914; May 1974; Sissenwine 1984; Peterman et al. 1988; Bradford 1992).

Accurate and precise measurements of population abundance are essential to estimating mortality rates, and the goal of survey design must be to minimize estimates of the variance in animal abundance while ensuring thorough coverage. We have demonstrated that this requires accurate knowledge of the effect that water masses may have on the distribution of animals, as well as consideration of the level of synopticity of the survey. If the basis for survey design is determined primarily by logistic constraints, then subsequent appraisal of the information obtained from such surveys may reveal that the precision achieved was not the most appropriate to address questions

Fig. 6. Simulated estimates of mean overall abundance (x_t) (top left) based on t days of sampling, the abundance of animals on day t (n_t) (center left), and their relative values (x_t/n_t) (bottom left) in relation to the duration of a survey for a model in which the numbers of a single cohort of animals (spawned at $t = 0$) are assumed to decrease exponentially with time according to $n_t = 10e^{-zt}$ (where z is the daily mortality rate; 0.05, dashed line; 0.10, dotted line; 0.20, dash-dotted line). Mean abundance is estimated as $x_t = 1/t \int_1^t n_t dt$. Abundance at $t = 0$ was set at 10 larvae·m^{-2}, the overall mean of our estimates from the nested survey in this study. Animals are assumed to be uniformly distributed throughout the survey area, but abundance estimates are subject to random sampling variability as estimated in this study. Average relative sampling variability (s_t/x_t) (top right) was estimated from the results of this study where $s_t^2 = 1.64x_t^{1.85}$. Total overall relative variability ($x_t^{-1}(v_n^2 + s_t^2)^{1/2}$) in estimated abundance was estimated by adding the variance in average numbers ($v_n^2 = (t-1)^{-1} \sum_{t=2}^{t} [n_t - x_t]^2$) to the sampling variability (s_t^2) (center right). Total and sampling variability are contrasted in the bottom right panel. Variance in abundance estimates caused by large-scale variations in the distribution of ichthyoplankton are not considered in these calculations.



dealing with variations in survivorship. Personnel, equipment, and monetary constraints clearly impose restrictions on survey design. However, there would be little benefit in conducting studies that are unlikely to yield information of the quality required to determine the underlying processes that regulate population dynamics during the early life stages. Sampling programs must be preceded by pilot studies designed to determine the effort required to obtain the most precise estimates of abundance, given limitations caused by the underlying sampling variability. It is essential to ensure that problems caused by sampling variability within strata are not compounded due to inappropriate spatial and temporal sampling of the population.

Acknowledgements

We wish to thank S. Akenhead, C. Fitzpatrick, R. Penney, B. Rodgers, T.H. Shears, and P. Stead for their assistance in various phases of the study. Special thanks go to the captains and crews of the *Gadus Atlantica*, *Newfoundland Hawk*, and CSS *Pandora* for their help and cooperation.

References

Akenhead, S.A. 1986. Water retention on Flemish Cap. *In* The role of freshwater outflow in coastal marine ecosystems. *Edited by* S. Skreslet. Springer-Verlag, Berlin. pp. 283–293.

Anderson, J.T. 1984. The early life history of redfish (*Sebastes* spp.) on Flemish Cap. Can. J. Fish. Aquat. Sci. **41**: 1106–1116.

Anderson, J.T. 1990. Seasonal development of invertebrate zooplankton on Flemish Cap. Mar. Ecol. Prog. Ser. **67**: 127–140.

Anderson, R.M., Gordon, D.M., Crawley, M.J., and Hassell, M.P. 1982. Variability in the abundance of animals and plant species. Nature (Lond.), **296**: 245–248.

Anonymous. 1978. Report of the environmental subcommittee. ICNAF Redbook, Appendix IV. pp. 93–94.

Anonymous. 1992. Study group on spatial and temporal integration. I.C.E.S. C.M. 1993/L:9.

Beyer, J. 1989. Recruitment stability and survival: simple size-specific theory with examples from the early life dynamics of marine fish. Dana Rep. **7**: 45–147.

Bradford, M.J. 1992. Precision of recruitment predictions from early life stages of marine fishes. Fish. Bull. U.S. **90**: 439–453.

Cassie, R.M. 1968. Sample design. *In* Reviews on zooplankton sampling methods. *Edited by* D.J. Tranter. Zooplankton sampling. UNESCO Monogr. Oceanogr. Methodol. **2**: 105–121.

Cochran, W.G. 1977. Sampling techniques. 3rd ed. John Wiley & Sons, New York.

Cyr, H., Downing, J.A., Lalonde, S., Baines, S.B., and Pace, M.L. 1992. Sampling larval fish populations: choice of sample number and size. Trans. Am. Fish. Soc. **131**: 356–368.

Downing, J.A. 1986. Spatial heterogeneity: evolved behaviour or mathematical artifact? Nature (Lond.), **323**: 255–257.

Downing, J.A. 1991.Biological heterogeneity in aquatic ecosystems. *In* Ecological heterogeneity. *Edited by* J. Kolosa and S.T.A. Pickett. Springer-Verlag, Berlin. pp. 160–180.

Downing, J.A., Pérusse, M., and Frenette, Y. 1987. Effect of interreplicate variance on zooplankton sampling design and analysis. Limnol. Oceanogr. **32**: 673–680.

Elliot, J.M. 1973. Some methods for the statistical analysis of samples of benthic invertebrates. Scientific publication No. 25. 2nd ed. Freshwater Biological Association, Ambleside, England.

Fortier, L., and Leggett, W.C. 1985. A drift study of larval fish survival. Mar. Ecol. Prog. Ser. **25**: 245–257.

Frank, K.T. 1988. Independent distribution of fish larvae and their prey: natural paradox or sampling artefact? Can. J. Fish. Aquat. Sci. **45**: 48–59.

Frank, K.T., and Leggett, W.C. 1985. Reciprocal oscillations in densities of larval fish and potential predators: a reflection of present and past predation? Can. J. Fish. Aquat. Sci. **42**: 1841–1849.

Frank, K.T., Carscadden, J.E., and Leggett, W.C. 1993. Causes of spatio-temporal variation in the patchiness of larval fish distributions: differential mortality or behaviour? Fish. Oceanogr. **2**: 114–123.

Greig-Smith, P. 1952. The use of random and contiguous quadrats in the study of structure of plant communities. Ann. Bot. **16**: 293–316.

Heath, M., and MacLachlan, P. 1987. Dispersion and mortality of yolk-sac herring (*Clupea harengus* L.) larvae from a spawning ground to the west of the Outer Hebrides. J. Plankton Res. **9**: 613–630.

Hewitt, R. 1981. The value of pattern in the distribution of young fish. Rapp. P.-v. Réun. Cons. int. Explor. Mer, **178**: 229–236.

Hewitt, R.P., Theilacker, G.H., and Lo, N.C.H. 1985. Causes of mortality in young jack mackerel. Mar. Ecol. Prog. Ser. **26**: 1–10.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-v. Réun. Cons. int. Explor. Mer, **20**: 1–228.

Houde, E.D. 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. **2**: 17–29.

Legendre, L., and Demers, S. 1984. Towards dynamic biological oceanography and limnology. Can. J. Fish. Aquat. Sci. **41**: 2–19.

Leggett, W.C. 1986. The dependence of larval fish survival on food and predators. *In* The role of freshwater outflow in coastal marine ecosystems. *Edited by* S. Skreslet. Springer-Verlag, Berlin. pp. 117–137.

Lo, N.C.H. 1985. Egg production of the central stock of northern anchovy 1951–1983. Fish. Bull. U.S. **83**: 137–150.

Lo, N.C.H. 1986. Modelling life-stage-specific instantaneous mortality rates, an application to northern anchovy, *Engraulis mordax*, eggs and larvae. Fish. Bull. U.S. **84**: 395–412.

Loder, J.W., Ross, C.K., and Smith, P.C. 1988. A space- and time-scale characterization of circulation and mixing over submarine banks, with application to the northwestern Atlantic continental shelf. Can. J. Fish. Aquat. Sci. **45**: 1860–1885.

Mackas, D.L., and Boyd, C.M. 1979. Spectral analysis of zooplankton spatial heterogeneity. Science (Washington, D.C.), **204**: 62–64.

Mackas, D.L., Denman, K.L., and Abbott, M.R. 1985. Plankton patchiness: biology in the physical vernacular. Bull. Mar. Sci. **37**: 652–674.

May, R.C. 1974. Larval mortality in marine fishes and the critical period concept. *In* The early life history of fish. *Edited by* J.H.S. Blaxter. Springer-Verlag, Berlin. pp. 3–20.

McGurk, M.D. 1989. Advection, diffusion, and mortality of Pacific herring larvae, *Clupea harengus pallasi*, in Bamfield Inlet, British Columbia. Mar. Ecol. Prog. Ser. **51**: 1–18.

Morse, W.W. 1989. Catchability, growth, and mortality of larval fish. Fish. Bull. U.S. **87**: 417–446.

Mullin, M.M., Brooks, E.R., Reid, F.M.H., Napp, J., and Stewart, E.F. 1985. Vertical structure of nearshore plankton off southern California: a storm and a larval fish food web. Fish. Bull. U.S. **83**: 151–170.

Munk, P., Christensen, V., and Paulsen, H. 1986. Studies of a larval herring (*Clupea harengus*) patch in the Buchan area. II. Growth, mortality, and drift of larvae. Dana Rep. **6**: 11–24.

Myers, R.A., and Pepin, P. 1990. The robustness of lognormal-based estimators of abundance. Biometrics, **46**: 1185–1192.

Myers, R.A., and Pepin, P. 1991. On testing the robustness of lognormal-based estimators. Biometrics, **47**: 1623–1624.

O'Connell, C.P. 1980. Percentage of starving northern anchovy larvae in the sea as estimated by histological methods. Fish. Bull. U.S. **78**: 475–489.

Pace, M.L., Findlay, S.E.G., and Lints, D. 1991. Variance in zooplankton samples: evaluation of a predictive model. Can. J. Fish. Aquat. Sci. **48**: 146–151.

Pepin, P. 1993. Application of empirical size-dependent models of larval fish vital rates to the study of production: accuracy and association with adult stock dynamics in a comparison among species. Can. J. Fish. Aquat. Sci. **50**: 53–59.

Peterman, R.M., Bradford, M.J., Lo, N.C.H., and Methot, R.D. 1988. Contribution of early life stages to interannual variability in recruitment of northern anchovy (*Engraulis mordax*). Can. J. Fish. Aquat. Sci. **45**: 8–16.

Pinel-Alloul, B., and Pont, D. 1991. Spatial distribution patterns in freshwater macrozooplankton: variation with scale. Can. J. Zool. **69**: 1557–1570.

Pinel-Alloul, B., Downing, J.A., Pérusse, M., and Codin-Blumer, G. 1988. Spatial heterogeneity in freshwater zooplankton: variation with body size, depth, and scale. Ecology, **69**: 1393–1400.

Platt, T., and Denman, K.L. 1975. Spectral analysis in Ecology. Annu. Rev. Ecol. Syst. **6**: 189–210.

Ross, C.K. 1980. Moored current meter data from Flemish Cap, January–July 1979. NAFO SCR. Doc. 80/IX/128, Ser. No. N200.

Sissenwine, M.P. 1984. Why do fish populations vary? *In* Exploitation of marine populations. Report of the Dalhem Workshop on Exploitation of Marine Communities, Berlin 1984. *Edited by* R.M. May. Springer-Verlag, Berlin. pp. 59–94.

Smith, P.E. 1973. The mortality and dispersal of sardine eggs and larvae. Rapp. P.-v. Réun. Cons. int. Explor. Mer, **164**: 282–292.

Smith, P.E. 1985. Year-class strength and survival of 0-group clupeoids. Can. J. Fish. Aquat. Sci. **42**(Suppl. 1): 69–82.

Smith, P.E., and Richardson, S.L. 1977. Standard techniques for pelagic egg and larval surveys. FAO Fish. Tech. Circ. No. 175.

Strickland, J.D.H., and Parsons, T.R. 1968. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. No. 167.

Talbot, J.W. 1977. The dispersal of plaice eggs and larvae in the Southern Bight of the North Sea. J. Cons. Cons. int. Explor. Mer, **37**: 221–248.

Tsuda, A., Sugisaki, H., Ishimaru, T., Saino, T., and Sato, T. 1993. White-noise-like distribution of the oceanic copepod *Neocalanus cristatus* in the subarctic north Pacific. Mar. Ecol. Prog. Ser. **97**: 39–46.

Weber, L.H., El-Sayed, S.Z., and Hampton, I. 1986. The variance spectra of phytoplankton, krill and water temperature on the Antarctic Ocean south of Africa. Deep-Sea Res. **33**: 1327–1343.

Young, T.L., and van Woert, M.L. 1991. Plott88 software library reference manual. Plotworks Inc., Ramona, Calif.

Zweifel, J.R., and Smith, P.E. 1981. Estimates of abundance and mortality of larval anchovies (1951–75): application of a new method. Rapp. P.-v. Réun. Cons. int. Explor. Mer, **178**: 248–259.

Analysis of harvest strategies for red king crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska

J. Zheng, M.C. Murphy, and G.H. Kruse

Abstract: A modifiable harvest rate constrained by a minimum spawning abundance (threshold) is currently used to set the annual harvest level for Bristol Bay red king crab, *Paralithodes camtschaticus*. A length-based simulation model was constructed to evaluate effects of recruitment, natural mortality, and handling mortality on this harvest strategy. Evaluation criteria included mean yield, stability of yield, harvest opportunity, and stability of spawning stock. Optimal mature male harvest rates were strongly negatively related to handling mortality. For any given harvest rate, handling mortality is a key factor influencing optimal thresholds. The current harvest strategy produces a high mean yield and low variability in yield under low handling mortality scenarios, but the population is at high risk of collapse with a high handling mortality. Given uncertainties of recruitment, natural mortality, and handling mortality estimates, we recommend reducing mature male harvest rate from 20 to 15% and maximum legal male harvest rate cap from 60 to 50%. If handling mortality rate is greater than 30%, then we recommend increasing the threshold from 6600 to 11 000 metric tons of effective spawning biomass. Our recommended harvest strategy produces a mean yield similar to the current harvest strategy and safeguards against recruitment overfishing.

Résumé : Un taux de récolte modifiable lié à une abondance de frai minimale (seuil) est actuellement utilisé pour établir le niveau de récolte annuel du crabe royal, *Paralithodes camtschaticus*, de la baie Bristol. Un modèle de simulation fondé sur la longueur a été élaboré pour évaluer les effets du recrutement, de la mortalité naturelle et de la mortalité liée à la manipulation sur cette stratégie de récolte. Les critères d'évaluation comprennent le rendement moyen, la stabilité du rendement, les occasions de récolte et la stabilité du stock de reproducteurs. Les taux de récolte optimaux des mâles à maturité présentaient une corrélation fortement négative avec la mortalité liée à la manipulation. Quel que soit le taux de récolte, la mortalité liée à la manipulation est un facteur clé influant sur les seuils optimaux. La stratégie de récolte actuelle entraîne un rendement moyen élevé et une faible variation du rendement dans des scénarios de faible mortalité liée à la manipulation, mais la population est fortement exposée à un effondrement si la mortalité liée à la manipulation est élevée. Étant donné les incertitudes touchant les estimations du recrutement, de la mortalité naturelle et de la mortalité liée à la manipulation, nous recommandons une réduction du taux de récolte des mâles à maturité de 20 à 15 % et un plafonnement du taux de récolte des mâles de taille légale de 60 à 50 %. Si la mortalité liée à la manipulation est supérieure à 30 %, nous recommandons alors d'augmenter le seuil de 6 600 à 11 000 tonnes métrique de biomasse de frai réelle. La stratégie de récolte que nous recommandons entraîne un rendement moyen semblable à celui de la stratégie de récolte actuelle et assure une protection contre la surpêche affectant le recrutement.
[Traduit par la Rédaction]

Introduction

Harvests of red king crab (RKC), *Paralithodes camtschaticus*, in Bristol Bay, Alaska, have been characterized by dramatic fluctuations in abundance. The fishery began in 1930 and was conducted primarily by the Japanese and Russians before 1971 (Otto 1986). During the late 1960s, the U.S. fishing fleet gradually expanded, and by 1974, all foreign fishing for RKC was phased out. The domestic fishery peaked in 1980 with a yield of 59 000 t (metric tons). The stock crashed and no fishing was allowed in 1983. Since 1984, yield and stock abundance have stayed at low levels (Griffin and Ward 1994; Stevens et al. 1994).

The Bristol Bay RKC fishery is cooperatively managed by the State of Alaska and the U.S. federal government. Two major management objectives for the fishery are to maintain a healthy stock that ensures reproductive viability and to provide for sustained levels of harvest over the long term that avoid fishery-induced boom-and-bust cycles (ADF&G 1994). In attempting to meet these objectives, management practices continue historical size–sex–season (3S) policies, i.e., harvest of males only ≥135 mm carapace length (CL) and no fishing during spring molting and mating periods (ADF&G 1994). In addition, fishing effort is controlled through vessel registration, pot limits, and other gear restrictions (ADF&G 1994). Catch is based on a modifiable harvest rate strategy constrained by a minimum spawning abundance. Under the current management plan, a 20% mature male harvest rate is applied to the abundance of mature (≥120 mm CL) males with a maximum 60% harvest rate cap of legal (≥135 mm CL) males (Pengilly and Schmidt 1995). The stock has been

Received November 22, 1994. Accepted October 7, 1996.
J12640

J. Zheng,[1] M.C. Murphy, and G.H. Kruse. Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, P.O. Box 25526, Juneau, AK 99802-5526, U.S.A.

---

[1] Author to whom all correspondence should be addressed. e-mail: jiez@fishgame.state.ak.us

assessed each year since 1968 by the National Marine Fisheries Service (NMFS) with a trawl survey conducted from May to August (Stevens et al. 1994). Recently, a length-based model was developed to improve abundance estimates (Zheng et al. 1995*a*).

The current mature male harvest rate and maximum legal male harvest rate for the Bristol Bay RKC fishery are based on results of a simulation study for the Kodiak RKC fishery (Schmidt and Pengilly 1990). Comprehensive computer simulation studies on optimal harvest strategies were conducted for the Bristol Bay RKC fishery by Balsiger (1974) and Reeves and Marasco (1980). Balsiger (1974) estimated the maximum equilibrium yield to be 11 400 t, which is less than the mean observed yield during the last three decades. Reeves and Marasco (1980) apparently overestimated productivity of Bristol Bay RKC and suggested an optimal yield of 50 000 t. In addition to lack of adequate information to estimate stock–recruitment (S–R) relationships and natural mortality, all previous simulation studies used deterministic models that could not be used to examine the risk of population collapse.

A threshold was added to existing management measures in 1990 to avert recruitment overfishing (Pengilly and Schmidt 1995). The threshold is defined as the minimum mature female abundance "that allows sufficient recruitment so that the stock can eventually reach a level that produces MSY (Maximum Sustained Yield)" (NPFMC 1989). If population size falls below the threshold value, no fishing is allowed.

A threshold of 8.4 million fertilized females was estimated for Bristol Bay RKC by applying Thompson's rule (Thompson 1993) of 20% equilibrium spawning stock to the Ricker S–R model (NPFMC 1990). In practice, 8.4 million mature (≥90 mm CL) females have been used as the threshold level (Pengilly and Schmidt 1995). Application of this estimation method may not be appropriate because (*i*) Thompson's rule was derived from strong depensatory S–R models whereas this crab stock was fit with traditional Ricker curves (NPFMC 1990) or weak depensatory S–R curves (Zheng et al. 1995*a*) that do not need thresholds according to Thompson's findings and (*ii*) this approach does not account for handling mortality of female and sublegal crab, which could be substantial and vary from year to year.

In recognition of these problems, we used an alternative method to define and estimate an optimal threshold level. We defined threshold differently as a percentage of pristine effective spawning biomass, SP_∞. Following Zheng et al. (1995*a*), effective spawning biomass was calculated from estimates of male reproductive potential and spawning female abundance. Male reproductive potential is the sum of mature male abundances by CL, each multiplied by the estimated maximum number of females with which a male of that particular CL can mate (Zheng et al. 1995*a*). The number of females induced to ovulate and the percentage of eggs fertilized depend on male body size (Paul and Paul 1990). Large mature males are able to mate multiple females during a mating season (Table 1).

Although the threshold concept has been applied to RKC fisheries in Bristol Bay and elsewhere in Alaska, a thorough evaluation of Alaskan threshold criteria and harvest levels has not been performed. The purpose of this study was to analyze harvest strategies for Bristol Bay RKC with different threshold levels and harvest rates under variable environmental conditions, several handling mortality rates, and different weights applied to different management objectives. We simulated RKC population dynamics by adding stochastic environmental effects to a length-based population model and an S–R model developed and updated by Zheng et al. (1995*a*, 1995*b*, respectively). A harvest model was used to simulate population and fishery outcomes from alternative parameterizations of three components of harvest strategy: threshold, mature male harvest rate, and maximum legal male harvest rate. We analyzed optimal levels of each component individually and in combination with each other in response to environmental variability, handling mortality rate, and management objective. Based on our findings, we formulated a new harvest strategy that is robust to these factors. We then conducted a sensitivity analysis of our robust strategy to structural errors in shape of the S–R curve, decadal-scale changes in natural mortality, and handling mortality rates.

Methods

Population parameters

The length-based population model used here is identical with that developed by Zheng et al. (1995*b*) and is summarized in the Appendix. Population parameters were obtained from Zheng et al. (1995*b*) and are summarized in Table 1. For convenience, all size measurements in this study are CL in millimetres. Population abundances were simulated annually during June each year, generally after RKC complete annual molting and mating in Bristol Bay. Fishing has occurred during the first 2 weeks of November each year since 1990. Thus, a lag of about 4.8 months, or 0.4 years, between abundance assessment and the fishery was used in our simulations.

S–R data for Bristol Bay RKC were also obtained from Zheng et al. (1995*b*) and were used to fit a four-parameter Ricker curve that combined two special cases of the general S–R model: a general Ricker curve that attributes change in recruitment to size of effective spawning biomass ($r1 > 1$ and $a1 = 0$; Appendix) and an autocorrelated Ricker curve that emphasizes recruitment changes as due to environmental causes ($r1 = 1$ and $a1 > 0$). The combined curve (Fig. 1) fit the data well ($R^2 = 0.62$, df = 15) and was used to conduct our simulations. Because the combined curve synthesizes two different, but potentially valid, interpretations of the data, sensitivity of the robust harvest strategy to these extremes was examined. Sex ratio of recruits was assumed to be 1:1.

Harvest model

Harvest procedure included comparison of stock status to threshold level, determination of a catch quota for legal crab, and estimation of deaths of sublegal and female crab due to handling. Annual effective spawning biomass, SP_t, was used to determine whether the population was above the threshold, T. If $SP_t \leq T$, then no fishing is allowed; otherwise, legal male harvest rate applied to legal crab ($l \geq 135$ mm CL), NL_t, is

$$(1) \qquad H_t = \min[E(NM_t/NL_t), MH]$$

where E is mature male harvest rate applied to NM_t, mature male abundance ($l \geq 120$ mm CL), and MH is maximum legal male harvest rate. Catch by length of legal male crab ($l \geq 135$ mm CL) is

$$(2) \qquad C_{l,t} = H_t(N_{l,t} + O_{l,t})$$

and total yield (TC_t) is obtained by multiplying by the corresponding weight at length and summing over all lengths:

$$(3) \qquad TC_t = \sum_l [C_{l,t} W_l], \quad l \geq 135 \text{ mm CL.}$$

Handling mortality was incorporated in the length-based model for female and sublegal male crab. We assumed that catchability for large

Table 1. Population parameters for a length-based model of Bristol Bay RKC (Zheng et al. 1995*b*) (see text and Appendix for parameter definitions).

Mid-CL (mm)	Weight (kg) Male	Weight (kg) Female	α_l Male	α_l Female	Max. female mates/male	Male molting probability
92.5		0.564		8.271	0.0	
97.5	0.696	0.634	28.902	7.734	0.0	0.980
102.5	0.815	0.709	28.902	7.197	0.0	0.969
107.5	0.948	0.789	28.902	6.660	0.0	0.953
112.5	1.094	0.873	29.287	5.800	0.0	0.928
117.5	1.256	0.962	29.480	5.048	0.0	0.893
122.5	1.432	1.056	29.480	4.511	1.0	0.842
127.5	1.625	1.155	29.672	4.189	1.2	0.773
132.5	1.835	1.258	29.865	3.867	1.4	0.686
137.5	2.063	1.367	30.058	3.437	1.6	0.583
142.5	2.310	1.480	30.250	2.148	1.8	0.472
147.5	2.576		30.443		2.1	0.364
152.5	2.862		30.636		2.4	0.264
157.5	3.169		30.829		2.7	0.190
162.5+	3.498		31.021		3.0	0.131

Growth parameter	Male	Female
a	13.14	16.49
b	0.018	–0.097
β	0.519	0.931

Natural mortality	Male	Female
Low	0.23	0.32
High	1.04	1.72

S–R relationship

Ricker model	General	Autocorrelated	Combined
*r*1	2.332	1.000	1.880
*r*2	−11.403	0.523	−7.396
*r*3	6.49×10^{-5}	2.05×10^{-5}	4.86×10^{-5}
k	7.000	7.000	7.000
*a*1	0.000	0.600	0.340
σ	0.700	0.700	0.700

Proportion by length	Male	Female
α_r	54.115	303.325
β_r	1.885	0.313

(≥90 mm CL) female and sublegal (95–134 mm CL) male crab was 50% of that for legal male crab. This value is close to observed bycatch rates in the Bristol Bay RKC fishery in 1990 and 1991 (Beers 1991, 1992). Thus, female deaths due to handling were assumed to be

$$(4)\qquad \mathrm{HD}_{\iota,t} = 0.5\, H_t F_{\iota,t}\mathrm{HM}$$

where HM is bycatch mortality rate. Deaths from handling for sublegal males are obtained by replacing female abundances with sublegal male abundances in eq. 4. Therefore, magnitude of handling mortality is a function of harvest rate and bycatch mortality rate.

To account for handling mortality of female crab, effective spawning biomass was updated after fishing by modifying eq. A6 to deduct handling mortality from female abundance:

$$(5)\qquad \mathrm{SP}_t = r_t \sum_{l} [(F_{\iota,t} - \mathrm{HD}_{\iota,t})\ \mathrm{WF}_l],\ \ \iota \geq 90 \text{ mm CL.}$$

Handling mortality for sublegal male crab was included in equations for male abundance by replacing catch, $C_{\iota,t}$, with deaths due to handling for $\iota = 95$–134 mm.

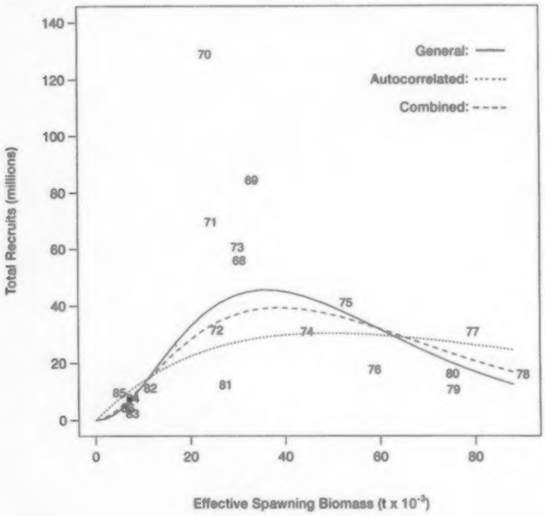
Population abundances and effective spawning biomasses were estimated with measurement error. Measurement error was assumed to be log-normally distributed (Zheng et al. 1993) with a coefficient of variation (CV) of 0.2. This was estimated for Bristol Bay legal RKC abundances using a bootstrapping approach with our length-based model (Zheng et al. 1995*b*). We assumed that implementation error was zero because a previous study on herring thresholds showed that implementation error is not important to optimal threshold levels (Zheng et al. 1993).

Simulations

Harvest strategies for Bristol Bay RKC were analyzed through computer simulations of population dynamics under different scenarios of threshold levels and harvest rates for the combined S–R curve. Based on previous experience (Zheng et al. 1993), we expected that optimal threshold levels would likely range from 0 to 50% of SP_∞. The current threshold is about 15% of SP_∞. The current harvest rate for mature male crab is 20%, but 10–40% is likely to cover the range of reasonable alternatives. Currently, the maximum legal male harvest rate is 60%, but reasonable alternatives may range from 40 to 80%. Simulated horizon was set as 5200 years, and statistics were collected only in the last 5000 years to reduce effect of initial conditions on results. Because we were interested in long-term population dynamics, we used a single replicate with a long horizon to estimate evaluation criteria. We evaluated each level of threshold and harvest rate in the simulations by a grid method. The grid interval was 5% for thresholds and mature male harvest rates and 10% for maximum legal male harvest rates.

The SP_∞ was estimated as the mean of effective spawning

Fig. 1. Relationships between total recruits at age 6.2 years (i.e., 7-year time lag) and effective spawning biomass for Bristol Bay RKC. Numbers refer to brood year. The data are from Zheng et al. (1995*b*).



biomasses without fishing under average environmental conditions. To ensure a stable estimate of SP_∞, simulated horizon was increased to 50 200 years and statistics in the last 50 000 years were used.

Currently, data are not available to estimate mortality of sublegal (95–134 mm CL) male and large (>89 mm CL) female RKC that are handled during commercial fisheries. Three handling mortality rates for crab bycatch were examined in this study: 0, 20, and 50%.

Three kinds of mechanisms are likely to cause a population collapse: a sudden increase in natural mortality, poor recruitment for an extended period, and overfishing. We introduced these mechanisms in the simulations by including time-variable natural mortality in the population model, autocorrelated recruitment in the S–R model, and high harvest rates up to 40% of mature male abundance in the harvest model.

Natural mortality for Bristol Bay RKC changes over time (Zheng et al. 1995*b*). Causes for this change are unknown, and we assumed that it is triggered by environmental conditions. Many environmental factors fluctuate with a cycle period from 12 to 24 years (Hollowed and Wooster 1992). Thus, we assumed two constant levels of instantaneous natural mortality (low and high, Table 1) with a cycle duration lasting 12–24 years: a low mortality for 10–20 years and then a switch to high mortality lasting for 2– 4 years. Durations for these periods were set randomly. Natural mortality patterns of RKC in Bristol Bay during the last two decades were similar to this scenario (Zheng et al. 1995*b*). A sensitivity study was conducted to examine effects of 10 different scenarios of natural mortality (Table 2) on a robust harvest strategy.

Simulations were initialized with a crab population of 50 million males (>94 mm CL) and 50 million females (>89 mm CL), an intermediate population size for the past 20 years. Length frequency distribution of the initial population was assumed that of Bristol Bay RKC in 1972. Identical seeds for random number generators were used for all scenarios to compare different harvest strategies under the same environmental conditions.

Evaluation criteria

Threshold management strategies for Bristol Bay RKC seek to protect stock reproductive potential and to achieve maximum long-term yield (NPFMC 1990; Pengilly and Schmidt 1995). These two objectives are related. If the stock is depressed, it is impossible to achieve maximum long-term yield. Conversely, maximum long-term yield is probably obtained when reproductive potential is optimal. A simple objective function described by Quinn et al. (1990) provides a tradeoff between long-term yield and variability in yield:

$$(6) \qquad \max\ [((1-\lambda)Y_i - \lambda \mathrm{SD}_i]$$

where Y_i and SD_i are mean and standard deviation of yield under management policy i and λ is a penalty weighting factor that measures the cost of one unit increase in variability in yield in terms of mean yield. Two special cases of this objective function are maximum mean yield ($\lambda = 0$) and equal tradeoff between mean yield and variability in yield ($\lambda = 0.5$). We used this objective function with $\lambda = 0$ and 0.5 as the primary criterion to estimate optimal threshold levels, mature male harvest rates, and maximum legal male harvest rates. Additional evaluation criteria included loss of harvest opportunity, expressed as a percentage of years the fishery is closed, and variability in effective spawning biomass.

Results

Pristine effective spawning biomass

Pristine effective spawning biomass was estimated using each of three S–R relationships to allow comparative sensitivity analyses. The general Ricker curve resulted in the highest SP_∞ (45 885.7 t) followed by the combined Ricker curve (43 949.3 t). The autocorrelated Ricker curve produced the lowest SP_∞ (36 720.8 t). The SP_∞ for the general Ricker curve and combined curve are higher because influence of strong year-classes at intermediate levels of effective spawning biomass is greater for these curves than the autocorrelated Ricker curve. Given the observed biomasses during the last two decades of extensive harvests, estimated SP_∞ for the autocorrelated Ricker curve may be too low.

Tradeoffs of using a threshold

Tradeoffs of different threshold levels under the current mature male harvest rate of 20% and maximum legal male harvest rate of 60% are illustrated in Fig. 2. With a handling mortality rate of 20% or less, effects of threshold on mean yield and variability in spawning biomass were very minor. However, increasing thresholds reduced fishing opportunity and increased annual variability in yield. Thus, there appears to be some cost but little benefit for using a threshold under these harvest rates and handling mortality rates. Under the scenario with a handling mortality rate of 50%, a threshold was important to protect the population and enhance long-term yield. Mean yield increased, and variability in effective spawning biomass was greatly reduced when a threshold was increased above 20% of SP_∞. With a handling mortality rate of 50%, a threshold at or above 20% of SP_∞ was required to prevent population collapse to zero abundance.

Optimal combinations of thresholds and mature male harvest rates

Optimal combinations of threshold levels and mature male harvest rates were evaluated for the current maximum legal harvest rate of 60% (Fig. 3). Objective function values were scaled to a maximum value of 1 and contours of values plotted as a function of threshold level and mature male harvest rate for each combination of weighting factor and handling mortality

Table 2. Period lengths, low and high values of natural mortality (*M*), and associated pristine effective spawning biomass (SP_∞) for 10 scenarios (A–J) of natural mortality used to evaluate the robust harvest strategy for Bristol Bay RKC (each scenario specifies a low and a high *M* and corresponding period lengths).

			Low *M*		High *M*		
Scenario	High period (years)	Low period (years)	Male	Female	Male	Female	SP_∞ ($t \times 10^{-3}$)
A	Constant over time		0.23	0.32	0.23	0.32	62.480
B	Constant over time		0.29	0.49	0.29	0.49	49.546
C	Constant over time		0.41	0.62	0.41	0.62	39.958
D	1–3	11–21	0.23	0.32	1.04	1.72	50.312
E	2–3	10–21	0.23	0.32	1.04	1.72	48.219
F	2–4	10–20	0.23	0.32	1.04	1.72	45.886
G	2–5	10–19	0.23	0.32	1.04	1.72	43.674
H	3–5	9–19	0.23	0.32	1.04	1.72	41.662
I	3–6	9–18	0.23	0.32	1.04	1.72	39.460
J	4–6	8–18	0.23	0.32	1.04	1.72	37.160

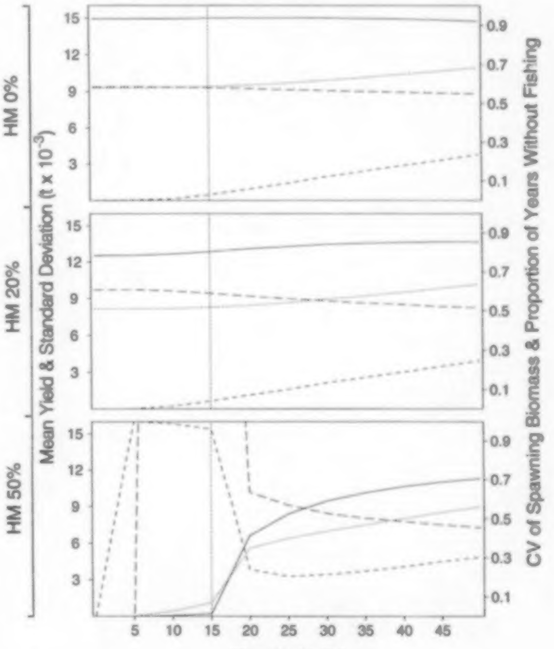
rate. With the maximum mean yield criterion ($\lambda = 0.0$), optimal threshold levels were 50% and optimal mature male harvest rates were negatively related to handling mortality rate (Fig. 3). For handling mortality rates of 0, 20, and 50%, optimal mature male harvest rates were 35, 25, and 20%, respectively. Without handling mortality, contour lines were flat across different threshold levels, indicating that a threshold was not needed. For high handling mortality rates (50%), contours were generally separated as two regions: an upper left region where high mature male harvest rate and low threshold level drove the population to collapse and a middle right region where a high threshold level helped achieve high yield. Between these two regions, yield changed dramatically (Fig. 3).

With the equal tradeoff criterion ($\lambda = 0.5$), optimal threshold levels varied from 10 to 25% under all scenarios (Fig. 3). Increased handling mortality rate reduced optimal mature male harvest rate. At low handling mortality rates (≤20%), objective function values were generally not affected by threshold levels between 0 and 25% as long as mature male harvest rates were close to 15–20% (Fig. 3).

The current harvest strategy achieves >85% of maximum objective function values possible with either maximum mean yield or equal tradeoff criterion if handling mortality rates are ≤20% (Fig. 3). The current harvest strategy is located near or at a very steep area of response surfaces with higher handling mortality rates (≥20%) and results in less than 30% of maximum objective function values with a 50% handling mortality rate (Fig. 3). Thus, risk of population collapse is high under uncertainty of handling mortality or unfavorable environmental conditions if more than half the crab that are returned to the sea due to sex or size restrictions die.

Either lower mature male harvest rates or higher threshold levels would reduce this risk. Lower mature male harvest rates would reduce mean yields under scenarios of low handling mortality (0–20%), but yields would be less sensitive to threshold level than those under the current mature male harvest rate. Higher thresholds would increase objective function values for scenarios of high handling mortality rates, yet cause little or no change in objective function values for low handling mortality rate scenarios. Thus, a lower mature male harvest rate and higher threshold level is a robust strategy to produce high yield and low risk of population collapse under all possible handling mortality scenarios considered.

Fig. 2. Mean yield (solid lines), standard deviation of yield (dotted lines), percentage of years without a fishery (short-dashed lines), and CV of effective spawning biomass (long-dashed lines) as a function of threshold level (% pristine effective spawning biomass) for Bristol Bay RKC under the current 20% mature male harvest rate and 60% maximum legal male harvest rate. Plots are classified by 0, 20, and 50% handling mortality rate (HM). Vertical dotted lines correspond to the current threshold level.

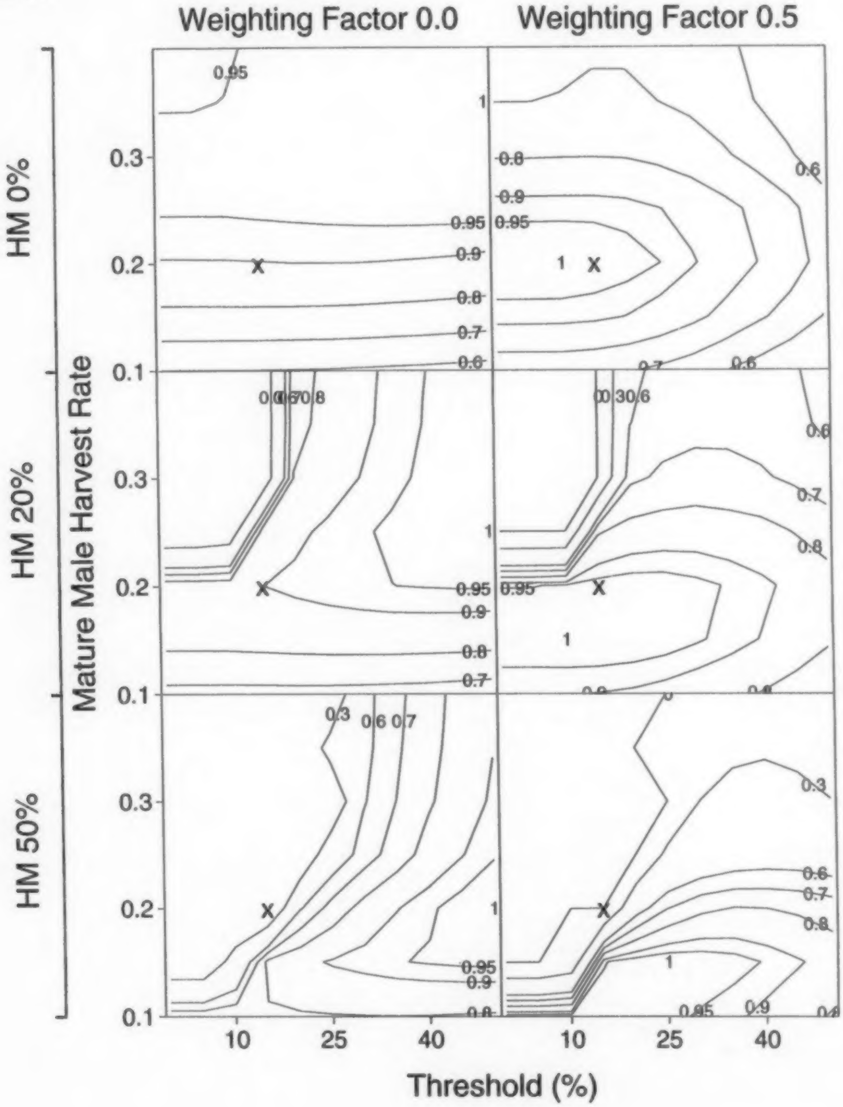


Optimal maximum legal male harvest rates

Next, we evaluated optimal maximum legal male harvest rates under alternative mature male harvest rates and thresholds. Optimal maximum legal male harvest rates were most dependent on management objectives and handling mortality (Fig. 4).

For the maximum yield criterion, maximum mean yields increased slightly when maximum legal male harvest rates

Fig. 3. Contour plots of the objective function by threshold level and mature male harvest rate for a 60% maximum legal male harvest rate for Bristol Bay RKC. Plots are classified by two weighting factors, λ = 0 and λ = 0.5, and 0, 20, and 50% handling mortality rates (HM). × = current harvest strategy.

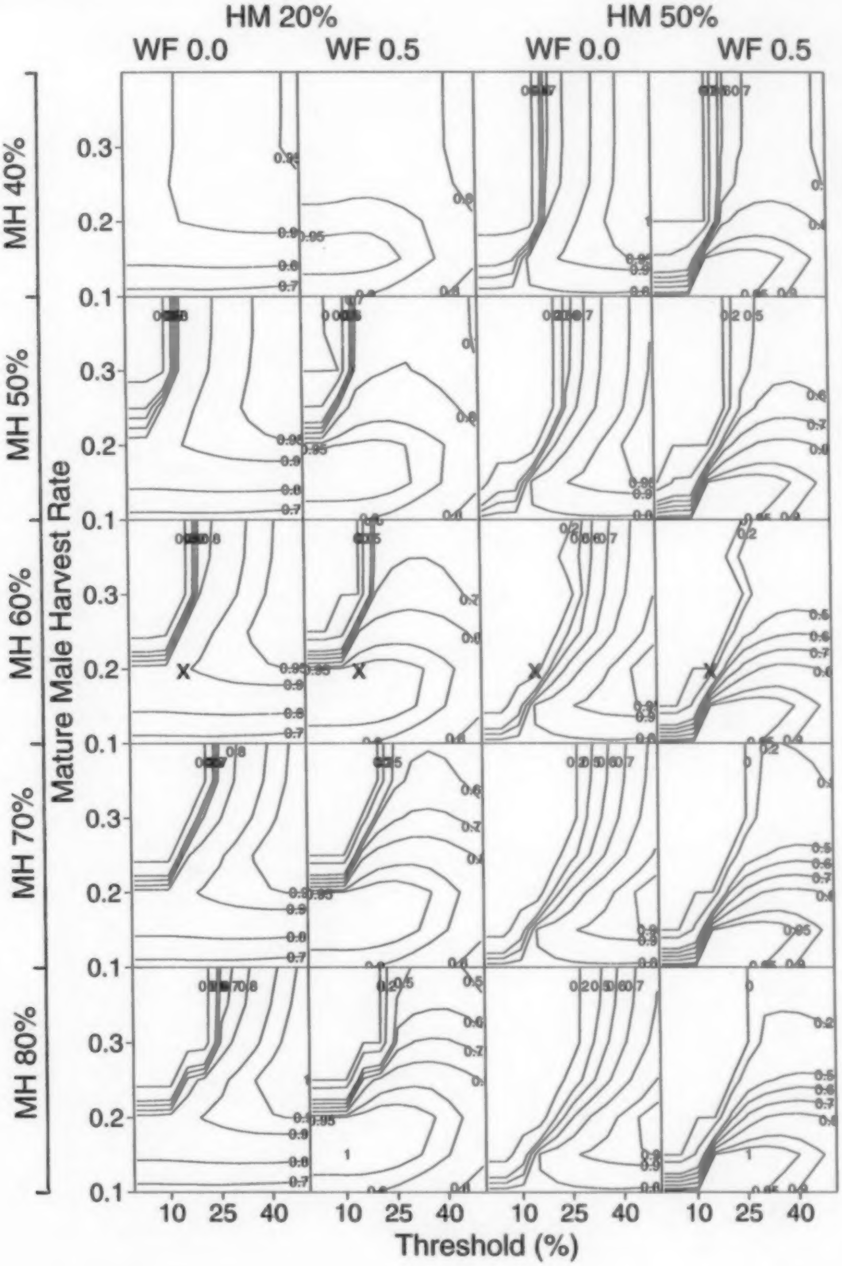


increased from 40 to 80% with a handling mortality rate of 20%. With a handling mortality rate of 50%, the maximum mean yield occurred with a maximum legal male harvest rate of 40% (Fig. 4). For both 20 and 50% handling mortality rates, response surfaces became flatter by decreasing maximum legal male harvest rates from 80 to 40%. Under all scenarios but one (20% handling mortality rate and 40% maximum legal male harvest rate), combinations of high mature male harvest rates and low threshold levels caused population collapse. The region susceptible to collapse increased with increasing maximum legal male harvest rate.

For the equal tradeoff criterion, maximum objective function values occurred with a maximum legal male harvest rate of 80% for both 20 and 50% handling mortality rates (Fig. 4). Response surfaces generally became flatter as maximum legal male harvest rates decreased from 80 to 40%.

Overall, for both criteria, a maximum legal male harvest rate of 40 or 50% generally resulted in a broader region for high objective values and a narrower region of population collapse than with maximum legal male harvest rates ≥60%. Maximum objective values were higher under a 50% maximum legal male harvest rate than under a 40% rate for both 20 and 50% handling mortality rates. Therefore, a maximum legal male harvest rate of 50% is the best choice.

Fig. 4. Contour plots of the objective function by threshold level and mature male harvest rate for Bristol Bay RKC. Plots are classified by 0.0 and 0.5 weighting factors (WF), 20 and 50% handling mortality rates (HM), and 40, 50, 60, 70, and 80% maximum legal male harvest rates (MH). × = current harvest strategy.



Optimal combinations of mature male and maximum legal male harvest rates and thresholds

Choice of management objective and handling mortality rate affected optimal combination of mature male harvest rate, maximum legal male harvest rate, and threshold. For the maximum yield criterion, both optimal mature male harvest rate and optimal maximum legal male harvest rate doubled when handling mortality rate decreased from 50 to 0% (Table 3). Optimal threshold levels were 50%, and the chance of fishery closure was greater than 28% under optimal strategies.

For the equal tradeoff criterion, optimal threshold levels increased from 10 to 25% and optimal mature male harvest

Table 3. Optimal mature male harvest rates (*E*), maximum legal male harvest rates (MH), threshold levels (TH), and associated mean yield and standard deviation of yield and percentage of the simulation years the fishery was closed for Bristol Bay RKC (HM = handling mortality rate).

	Optimal						Current: $E = 20\%$, MH = 60%			
HM (%)	*E* (%)	MH (%)	TH (%)	Yield ($t \times 10^{-3}$)	SD ($t \times 10^{-3}$)	Closed (%)	TH (%)	Yield ($t \times 10^{-3}$)	SD ($t \times 10^{-3}$)	Closed (%)
Maximum yield criterion ($\lambda = 0$)										
0	40	80	50	17.958	15.780	32.2	25	15.001	9.649	8.6
20	25	80	50	14.386	11.332	28.5	45	13.659	9.822	21.8
50	20	40	50	11.438	9.119	28.7	50	11.263	8.957	30.4
Equal tradeoff criterion ($\lambda = 0.5$)										
0	20	80	10	15.005	9.194	0.7	10	14.934	9.309	0.7
20	15	80	10	11.870	7.055	0.6	20	13.071	8.429	7.1
50	15	80	25	10.213	6.419	10.5	35	10.095	7.482	23.2

Table 4. Comparisons of mean yield, standard deviation of yield, CV of effective spawning biomass (SP), percentage of years without fishing (closed), and ranges of closed and open durations by handling mortality rate (HM) for the current harvest strategy (20% mature male harvest rate, 60% maximum legal male harvest rate, and a threshold of 6600 t of effective spawning biomass) and the robust strategy (15% mature male harvest rate, 50% maximum legal male harvest rate, and a threshold of 11 000 t) for Bristol Bay RKC (historical mean yield and its standard deviation included for comparison).

HM (%)	Yield ($t \times 10^{-3}$)	SD ($t \times 10^{-3}$)	CV SP (%)	Closed (%)	Closed duration (years)	Open duration (years)
Current strategy						
0	14.965	9.371	58.1	2.8	1–3	1–177
20	12.839	8.270	58.9	4.0	1–4	1–238
50[a]	3.098	2.951	79.8	38.6	1–9	1–16
Robust strategy						
0	12.888	8.038	56.3	7.6	1–5	1–173
20	12.080	7.478	55.1	8.1	1–6	1–173
50	10.280	6.528	54.5	10.3	1–5	1–101

Historical yield

Period	Yield ($t \times 10^{-3}$)	SD ($t \times 10^{-3}$)
1953–1994	13.907	13.169
1960–1994	15.737	13.705
1972–1994	15.031	15.788

[a] The population was not sustainable for this scenario. Statistics were computed using results before the population collapsed to zero abundance (493 years).

rates decreased from 20 to 15% when handling mortality rates increased from 0 to 50% (Table 3). Optimal maximum legal male harvest rate (80%) was not affected by handling mortality rate. Mean yield decreased 11–17% under the equal tradeoff criterion compared with that under the maximum yield criterion, but this loss was more than compensated by benefits of a 30–42% reduction in variability in yield and a 63–98% reduction in proportion of years without fishing.

When the maximum yield criterion was applied to the current 20% mature male harvest rate and 60% maximum legal male harvest rate, optimal threshold levels ranged from 25% under scenarios of no handling mortality to 50% with a 50% handling mortality rate (Table 3). For all scenarios, yield was lower under current harvest rates than under optimal levels, especially for no or low handling mortality. Proportions of years without fishing were much more variable under current harvest rates than under optimal strategies for different scenarios of handling mortality.

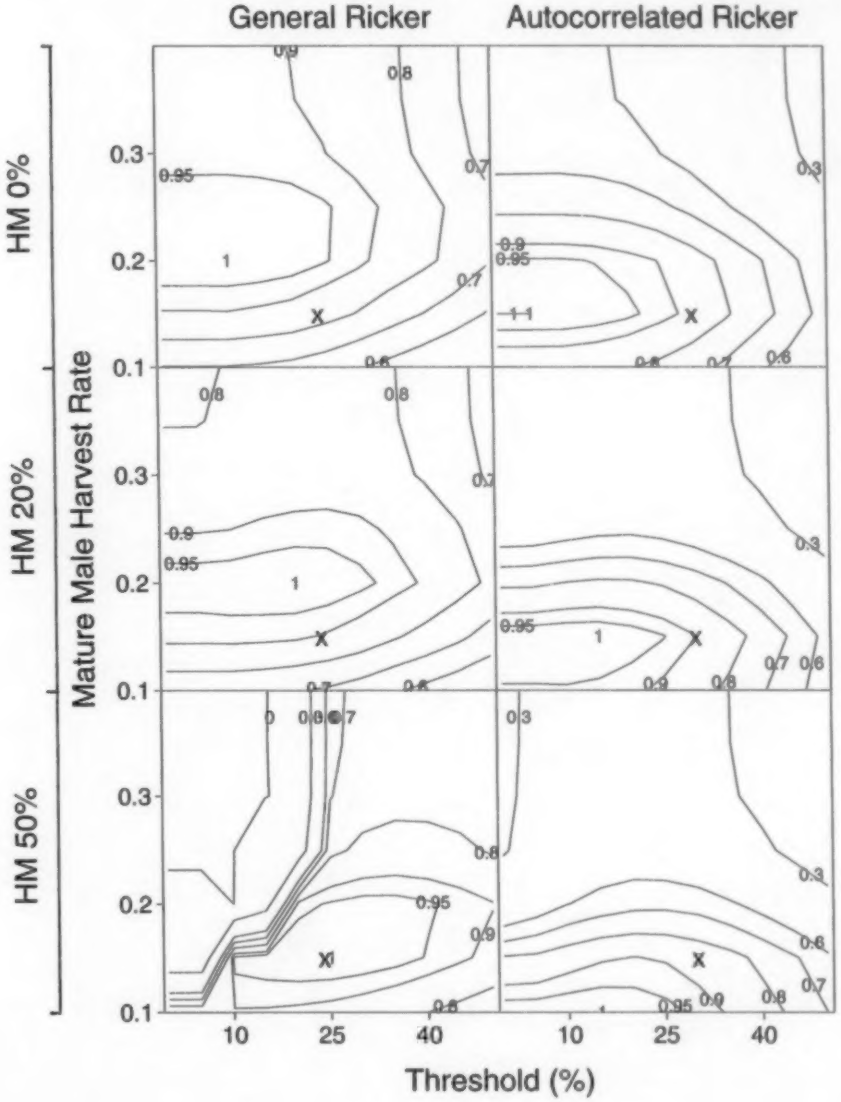
When the equal tradeoff criterion was applied to current harvest rates, optimal threshold levels increased from 10 to 35% as handling mortality rates increased from 0 to 50%. Proportions of years without fishing were much higher under current harvest rates than under optimal strategies for scenarios with handling mortality rates ≥20%.

A robust harvest strategy

From our results so far, we formulated a harvest strategy that is robust under uncertainties of recruitment and high natural and handling mortalities. Simulations indicated that a combination of a 15% mature male harvest rate, a 50% maximum legal male harvest rate, and a threshold level of 11 000 t (25%) of effective spawning biomass produced a high mean yield with low variability while providing protection of crab reproductive potential. The current mature male harvest rate of 20% is close to the mean rate from 1972 to 1978. Higher mature male harvest rates were observed after this time period during the late 1970s and early 1980s; this was followed by a precipitous decline in population abundance in the early 1980s (Zheng et al. 1995*a*). A maximum legal male harvest rate of 50% is lower than the current rate of 60%, but actual legal male harvest rates during 1972–1993 exceeded 50% only twice (Zheng et al. 1995*a*). Our results also showed that a 20% mature male harvest rate resulted in harvest of 47% of legal crab abundance, while a 15% mature male harvest rate produced a 32% legal male harvest rate. A threshold of 11 000 t is 67% higher than the current threshold level of 6600 t of effective spawning biomass (8.4 million mature females).

Mean yield was slightly higher with the current harvest strategy than for the robust strategy with scenarios of low handling mortality rates (Table 4). However, mean yield was much higher for the robust strategy than with the current strategy under scenarios with a high handling mortality rate (50%). Percentages of years without fishing were in general higher for the robust strategy than with the current strategy (Table 4). Variability in yield and effective spawning biomass was slightly lower for the robust strategy, so population production

Fig. 5. Contour plots of the equal tradeoff objective function by threshold level and mature male harvest rate for a 50% maximum legal male harvest rate for Bristol Bay RKC. Plots are classified by a general and an autocorrelated Ricker S–R curve and 0, 20, and 50% handling mortality rates (HM). × = robust harvest strategy (15% mature male harvest rate, 50% maximum legal male harvest rate, and a threshold of 11 000 t).



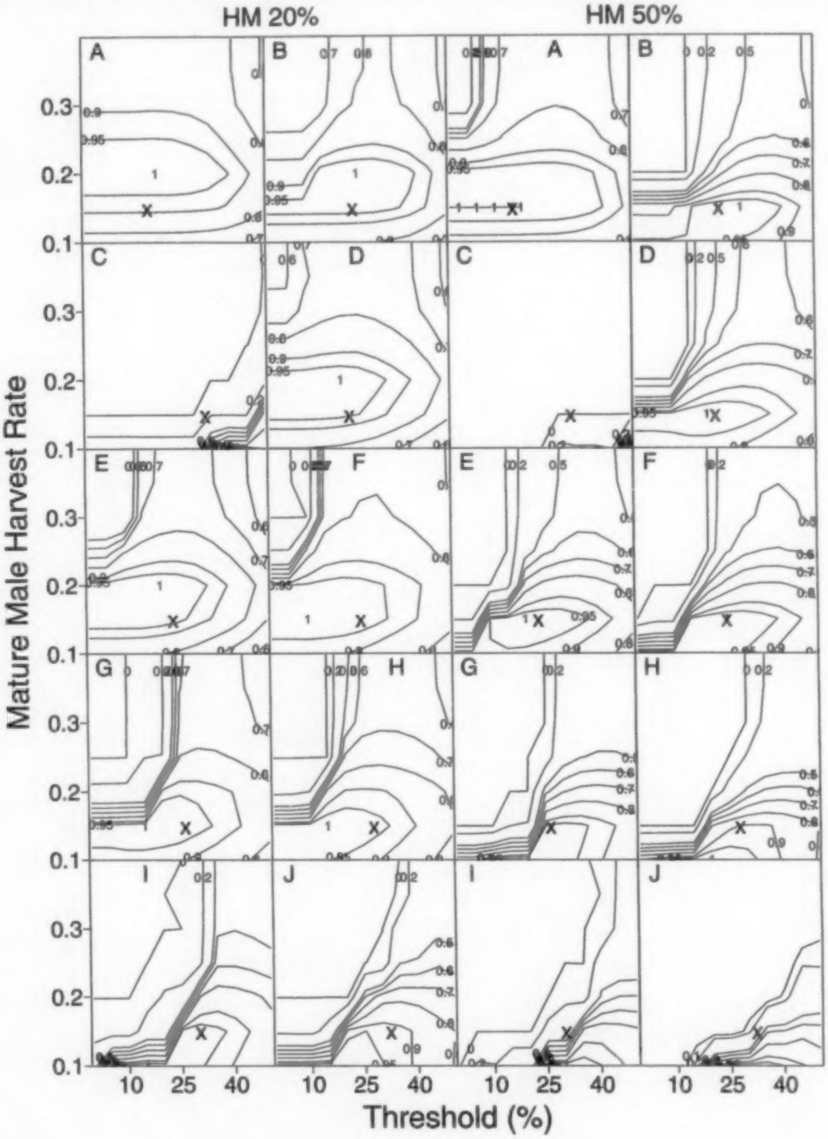
was more stable. Actual variability in yield during the last four decades was higher than results from our simulation study (Table 4) because historical harvest rates changed over time.

Sensitivity of robust harvest strategy to dynamics of S–R curves, natural mortality, and handling mortality

Sensitivity of the robust harvest strategy to dynamics of S–R relationships was examined using the equal tradeoff criterion for the general Ricker curve and autocorrelated Ricker curve (Fig. 5). As expected, results from these two S–R curves bracket our results from the combined curve (Fig. 3, right-hand panels) that includes both density-dependent and autocorrelated environmental effects. Overall, benefits of a threshold to long-term yield and population conservation were greater with the general Ricker curve than with the autocorrelated Ricker curve because recruitment success with the former is more influenced by spawning stock. With the general Ricker curve, the stock was much more vulnerable to overfishing under high handling mortality rates. Under all scenarios considered, the robust harvest strategy was located in or near flat areas of the response surfaces and produced more than 80% of the possible maximum objective function values (Fig. 5).

Interannual variation of natural mortality is still a major source of uncertainty in a simulation study to evaluate crab

Fig. 6. Contour plots of the equal tradeoff objective function by threshold level and mature male harvest rate for Bristol Bay RKC. Plots are classified by 20 and 50% handling mortality rates (HM) and 10 scenarios (A–J) of natural mortality (see Table 2). × = robust harvest strategy.

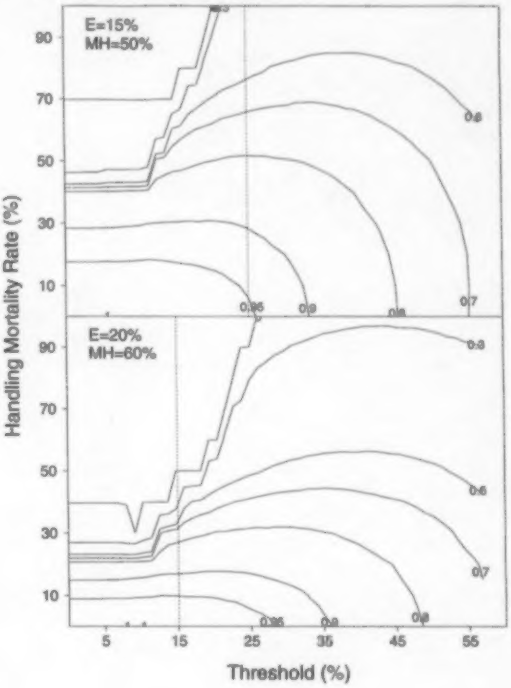


harvest strategies. Effects of natural mortality on the robust harvest strategy were examined with the equal tradeoff criterion and the combined S–R curve for 10 different scenarios of natural mortality (Table 2), ranging from very low to extremely high mortality (Fig. 6). With a 20% handling mortality rate, the strategy was very robust to natural mortality and achieved more than 90% of maximum objective values possible for all scenarios except scenario C (Fig. 6). With a 50% handling mortality rate, the strategy was robust to all except three high natural mortality scenarios, C, I, and J (Fig. 6). The likelihood that a 50% handling mortality rate has occurred with one of these high natural mortalities during the history of this fishery is low because this combination would result in mortality rates much higher than the mean mortality rate that we estimated over the past three decades (Zheng et al. 1995*a*, 1995*b*). Thus, it appears that the robust harvest strategy would result in 90% or more of the possible maximum objective function values under likely scenarios of natural mortality.

Last, we compared the performance of the robust harvest strategy and current harvest strategy with respect to uncertainty of handling mortality rate (Fig. 7). The robust strategy was located in the relatively flat area of the response surface over all handling mortality rates. When handling mortality rates were <70%, the robust strategy achieved more than 60%

of the maximum objective function values possible. In comparison, objective function values declined dramatically when handling mortality rates exceeded 30% under the current harvest strategy (Fig. 7). For a given mature male harvest rate, a high handling mortality rate needs to be compensated with a high optimal threshold level that functions as an alternative means to reduce total fishing mortality. Handling mortality rate is thus a key factor in determining optimal threshold level for a given mature male harvest rate.

Fig. 7. Contour plots of the equal tradeoff objective function by threshold level and handling mortality rate with 15 and 20% mature male harvest rates (E) and 50 and 60% maximum legal male harvest rates (MH) for Bristol Bay RKC. Vertical dotted lines correspond to threshold levels for the robust (upper plot) and current (bottom plot) harvest strategies.



Discussion

A harvest strategy for a fishery is highly dependent on both management objectives and recruitment dynamics of the population (Quinn et al. 1990; Zheng et al. 1993). When the objective is to maximize yield, optimal harvest strategy is both a high harvest rate and a high threshold level. Together, these cause pulse fishing, with corresponding high variability in yield and economic instability. On the other hand, when low variability in yield is as important as mean yield level, optimal harvest rate and threshold level must be set at intermediate levels. Although mean yield is slightly less than maximum yield for an equal tradeoff objective, lower harvest rates reduce variability in yield and the fishery is closed much less often. Use of a threshold helps to conserve a population, enhance long-term yield, and provide management flexibility.

The Alaska Board of Fisheries policy on king crab management is best approximated by the equal tradeoff criterion in which yield and variability in yield are weighted equally (ADF&G 1994). Among other objectives, the policy strives to provide for a sustained and reliable supply of high-quality product, substantial and stable employment, minimum risk of stock collapse, and maintenance of fisheries on multiple ages and sizes of crab. The Board recognized that this policy "may not result in maximization of physical or economic yield" (ADF&G 1994).

We assumed a low level of first-order autocorrelation for the combined S–R curve. However, if RKC recruitment in Bristol Bay is not only depensatory at low stock sizes but is more strongly autocorrelated than we assumed, then we have underestimated the frequency of population collapses and the length of time that the population is depressed. One mechanism for strong autocorrelation could be a sudden switch from favorable to unfavorable environmental conditions and vice versa, where each trend continues for a long time, e.g., from 6 to 12 years (Hollowed and Wooster 1992). In such cases, a high threshold is required to save enough spawning stock until favorable environmental conditions occur. Although we did not examine such strong recruitment autocorrelations, we found that a threshold management strategy is optimal when similar cycles occur in natural mortality. Effects of environmental conditions on recruitment of Bristol Bay RKC are currently being investigated (Tyler and Kruse 1996), and results should be incorporated into future studies of harvest strategies.

Handling mortality reduces future recruitment to the fishery by reducing both survival of prerecruits and effective spawning biomass due to deaths of mature females and sublegal males. Besides mortality, handling may also produce sublethal effects on crab such as reduced growth (Kruse 1993). To estimate handling mortality, we assumed a 50% catchability for sublegal male and large female crab, based on overall observed bycatch rates for the Bristol Bay RKC fishery in 1990 and 1991 (Beers 1991, 1992). However, bycatch catchability in 1992 and 1993 was near 100% (Tracy 1994). Increased bycatch catchability is probably attributable to reduced soak time resulting from shorter fishing periods and 250-pot limit per boat starting in 1992. Increase of pot mesh size from 19.7 to 22.9 cm for at least one third of one vertical surface of pot, starting in 1995, may nullify the effect of pot limitation and result in a bycatch catchability closer to 50%. If bycatch catchability is higher than 50%, total mortality rate for prerecruits and large females is underestimated in our study. Furthermore, crab near legal size may be more likely to be caught as bycatch. Unfortunately, data to compute length-dependent catchability were unavailable.

We examined a wide range of handling mortality rates for Bristol Bay RKC. Handling mortality rates may depend on handling injury, air temperature, wind speed, shell condition, and numerous other factors (Kruse 1993; Murphy and Kruse 1995). Exposure of RKC to cold air reduces vigor, lowers growth, and leads to increased mortality during ecdysis in severe situations (Carls and O'Clair 1990). Such effects could be significant during extremely cold weather during winter fisheries in some years. We estimated that average exposure of RKC to cold air during November fisheries during cold years would be milder than –1 C degree-hour which leads to handling mortality rates of 20% or less (Carls and O'Clair

1990). Unwanted crab are normally returned to the sea within 4 min (Zhou and Shirley 1996), and the coldest mean November air temperature at St. Paul, Alaska (near fishing grounds), during the history of the fishery was –2.1°C in 1987. However, historically the fishery extended longer into January through March when cold air exposure is more severe. Further, chill effects due to high wind in some years may cause higher handling mortality rates.

On the other hand, simulated deck and water impacts caused no increase in mortality of RKC, although injuries to spine and rostrum increased with handling (Zhou and Shirley 1995, 1996). Water impact was dismissed as a cause of mortality because recovery rates of tagged RKC during the fishery in 1993 were not significantly different among release methods (Watson and Pengilly 1994).

Not all potential factors contributing to handling mortality have been adequately studied (Kruse 1993; Murphy and Kruse 1995), so the level of handling mortality experienced in the Bristol Bay RKC fishery remains uncertain. For instance, effects of handling and habitat dislocation on predation mortality are unknown. Further, some crab receive abnormal treatment (e.g., dropped from height on deck, stepped on, left on deck for long periods) that may cause death or increase susceptibility to disease and subsequent death. Given uncertainties, we believe that handling mortality rates of 10–20% may be a reasonable assumption for purposes of our analysis. We have considered handling mortality rate as high as 50% to gauge potential handling effects that might have occurred historically in some years or from other effects that have yet to be corroborated by research. For frame of reference, the combination of a 50% catchability, 40% legal male harvest rate, and 50% handling mortality rate causes a 10% annual handling mortality rate for sublegal male and large female crab in the population.

Because of its importance to management strategy, we recommend the following research on handling mortality. First, ongoing collection and analysis of observer data provide improved estimates of bycatch catchability for female and sublegal male crab in response to changing regulations and fishing techniques. Second, air temperatures and wind speeds during the history of the fishery could be analyzed with respect to records of dead crab in landings statistics to estimate the significance of cold air exposure to stock declines. Third, effects of handling and habitat dislocation on predation mortality need to be specifically investigated. Finally, an alternative approach is to design a crab pot that reduces bycatch catchability, thereby minimizing handling mortality rate.

We did not evaluate two important aspects of the current harvest strategy for Bristol Bay RKC: size limits and sex restrictions. Thus, harvest strategies that we obtained may be still suboptimal. Large male crab get a higher price per unit of weight than small male crab (Bibb and Matulich 1994). In addition, processors avoid smaller crab because processing costs per pound vary inversely with crab size and because presence of smaller crab on the market depresses the price of larger crab (Bibb and Matulich 1994). Similarly, there is less economic incentive to harvest female crab which are smaller on average than the majority of male crab. Therefore, size limits and sex restrictions are based not only on considerations of stock spawning biomass, but also on fishery economics.

Handling mortality is linked to size and sex restrictions. Harvest of females and reduction of male size limit would reduce handling mortality and lead to lower optimal threshold levels. However, to develop an optimal "keep what you catch" harvest strategy with minimal bycatch would require a dynamic, bioeconomic model that incorporates size–price data by sex that are currently unavailable. Moreover, future bioeconomic analyses of female harvests should incorporate structural shifts in market economics resulting from potential sales of live, roe-bearing crab.

Given current size limits and sex restrictions, we recommend changing the current harvest strategy by reducing mature male harvest rate from 20 to 15% and maximum legal male harvest rate from 60 to 50%. Based on our belief that handling mortality rates may be 10–20% or so, no change in the current threshold level is warranted. However, if concerns exist that handling mortality rate is greater than 30%, the threshold level needs to be increased from 6600 to 11 000 t of effective spawning biomass. Our recommended strategy is robust to the uncertainties in handling mortality, S–R relationship, and environmental effects on recruitment and natural mortality that we examined in this study.

RKC tend to have life history traits that are identified with the stereotype of a *K*-selected species (Kruse 1993). High age-at-maturity, low frequency of strong year-classes, time-variable natural mortality, and compact aggregations render RKC exceptionally vulnerable to recruitment overfishing. Once the population collapses, it may take a long time to recover. If year-class strengths are affected by depensatory predation mortality, as evidenced by the general S–R relationship (Blau 1986; Zheng et al. 1995*a*), recovery of depressed stocks is difficult. A decade after the two largest RKC populations in Alaska crashed, Bristol Bay RKC are still at historically low levels and Kodiak RKC have not shown signs of recovery.

If population collapse is not due to overfishing, it may be impossible for any management strategy to prevent population collapse. However, since overfishing may possibly be a cause of collapse, it is prudent to minimize chance of collapse by preventing overfishing through harvest controls. When combined with harvest rate strategy, the threshold approach enhances long-term yield and is robust to management errors and uncertainties in population dynamics and environmental effects.

Acknowledgments

We thank Dana Schmidt, Doug Eggers, Doug Pengilly, Ivan Vining, and two anonymous reviewers for their comments on the manuscript. This study was funded in part by cooperative agreement NA37FL0333 from the National Oceanic and Atmospheric Administration. The views expressed herein are those of the authors and do not necessarily reflect the views of the National Oceanic and Atmospheric Administration or any of its subagencies.

References

Alaska Department of Fish and Game (ADF&G). 1994. Shellfish fishing regulations, 1994–95 edition. Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Juneau, Alaska.

Balsiger, J.W. 1974. A computer simulation model for the eastern Bering Sea king crab. Ph.D. dissertation, University of Washington, Seattle, Wash.

Beers, D.E. 1991. A summary of data contained in the mandatory crab observer database. Alaska Dep. Fish Game Commer. Fish. Div. Kodiak Reg. Inf. Rep. 4K91-14.

Beers, D.E. 1992. Annual biological summary of the shellfish observer database, 1991. Alaska Dep. Fish Game Commer. Fish. Div. Kodiak Reg. Inf. Rep. 4K92-33.

Bibb, S.A., and Matulich, S.C. 1994. Reducing the size limit on Alaska red king crab: price and revenue implications. Alaska Fish. Res. Bull. **1**(1): 1–9.

Blau, S.F. 1986. Recent declines of red king crab (*Paralithodes camtschatica*) populations and reproductive conditions around the Kodiak Archipelago, Alaska. *In* North Pacific Workshop on Stock Assessment and Management of Invertebrates. *Edited by* G.S. Jamieson and N. Bourne. Can. Spec. Publ. Fish. Aquat. Sci. No. 92. pp. 360–369.

Carls, M.G., and O'Clair, C.E. 1990. Influence of cold air exposures on ovigerous red king crabs (*Paralithodes camtschatica*) and Tanner crabs (*Chionoecetes bairdi*) and their offspring. *In* Proceedings of the International Symposium on King and Tanner Crabs. Alaska Sea Grant Rep. 90-04. pp. 329–343.

Griffin, K.L., and Ward, M.L. 1994. Annual management report for the shellfish fisheries of the Bering Sea area, 1992. *In* Annual management report for the shellfish fisheries of the westward region, 1992. Alaska Dep. Fish Game Commer. Fish. Div. Kodiak Reg. Inf. Rep. 4K94-9. pp. 131–183.

Hollowed, A.B., and Wooster, W.S. 1992. Variability of winter ocean conditions and strong year classes of Northeast Pacific groundfish. ICES Mar. Sci. Symp. **195**: 433–444.

Kruse, G.H. 1993. Biological perspectives on crab management in Alaska. *In* Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations. *Edited by* G.H. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn II. Alaska Sea Grant Rep. 93-02. pp. 355–384.

Murphy, M.C., and Kruse, G.H. 1995. An annotated bibliography of capture and handling effects on crabs and lobsters. Alaska Fish. Res. Bull. **2**(1): 76–80.

North Pacific Fishery Management Council (NPFMC). 1989. Fishery management plan for the commercial king and Tanner crab fisheries in the Bering Sea/Aleutian Islands. North Pacific Fishery Management Council, Anchorage, Alaska.

North Pacific Fishery Management Council (NPFMC). 1990. Environmental assessment for amendment 1 to the fishery management plan for the commercial king and Tanner crab fisheries in the Bering Sea/Aleutian Islands. North Pacific Fishery Management Council, Anchorage, Alaska.

Otto, R.S. 1986. Management and assessment of eastern Bering Sea king crab stocks. *In* North Pacific Workshop on Stock Assessment and Management of Invertebrates. *Edited by* G.S. Jamieson and N. Bourne. Can. Spec. Publ. Fish. Aquat. Sci. No. 92. pp. 83–106.

Paul, J.M., and Paul, A.J. 1990. Breeding success of sublegal size male red king crab *Paralithodes camtschatica* (Tilesius, 1815) (Decapoda, Lithodidae). J. Shellfish Res. **9**: 29–32.

Pengilly, D., and Schmidt, D. 1995. Harvest strategy for Kodiak and Bristol Bay red king crab and St. Matthew Island and Pribilof blue king crab. Alaska Dep. Fish Game Commer. Fish. Div. Juneau Spec. Publ. No. 7.

Quinn, T.J. II, Fagen, R., and Zheng, J. 1990. Threshold management policies for exploited populations. Can. J. Fish. Aquat. Sci. **47**: 2016–2029.

Reeves, J.E., and Marasco, R. 1980. An evaluation of alternate management options for the Southeastern Bering Sea king crab fishery. Northwest Alaska Fisheries Center, Processed Rep. 80-6. National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, WA 99115, U.S.A.

Schmidt, D., and Pengilly, D. 1990. Alternative red king crab fishery management practices: modelling the effects of varying size–sex restrictions and harvest rates. *In* Proceedings of the International Symposium on King and Tanner Crabs. Alaska Sea Grant Rep. 90-04. pp. 551–566.

Stevens, B.G., Haaga, J.A., and MacIntosh, R.A. 1994. Report to industry on the 1994 eastern Bering Sea crab survey. Alaska Fisheries Science Center, Processed Rep. 94-07. National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, WA 99115, U.S.A.

Thompson, G.G. 1993. A proposal for a threshold stock size and maximum fishing mortality rate. *In* Risk evaluation and biological reference points for fisheries management. *Edited by* S.J. Smith, J.J. Hunt, and D. Rivard. Can. Spec. Publ. Fish. Aquat. Sci. No. 120. pp. 303–320.

Tracy, D.A. 1994. Alaska Department of Fish and Game biological summary of the 1992 mandatory shellfish observer program database. Alaska Dep. Fish Game Commer. Fish. Div. Kodiak Reg. Inf. Rep. 4K94-10.

Tyler, A.V., and Kruse, G.H. 1996. A conceptual model of processes influencing the formation of year-class strength of red king crab in waters off Alaska. *In* High latitude crabs: biology, management, and economics. Alaska Sea Grant Rep. 96-02. pp. 511–544.

Watson, L.J., and Pengilly, D. 1994. Effects of release method on recovery rates of tagged red king crabs *Paralithodes camtschaticus* in the 1993 Bristol Bay commercial fishery. Alaska Dep. Fish Game Commer. Fish. Div. Kodiak Reg. Inf. Rep. 4K94-40.

Zheng, J., Funk, F.C., Kruse, G.H., and Fagen, R. 1993. Evaluation of threshold management strategies for Pacific herring in Alaska. *In* Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations. *Edited by* G.H. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn II. Alaska Sea Grant Rep. 93-02. pp. 141–166.

Zheng, J., Murphy, M.C., and Kruse, G.H. 1995*a*. A length-based population model and stock–recruitment relationships for red king crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska. Can. J. Fish. Aquat. Sci. **52**: 1229–1246.

Zheng, J., Murphy, M.C., and Kruse, G.H. 1995*b*. An update of length-based population model and stock–recruitment relationships for red king crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska. Alaska Fish. Res. Bull. **2**(2): 114–124.

Zhou, S., and Shirley, T.C. 1995. Effects of handling on feeding, activity and survival of red king crabs, *Paralithodes camtschaticus* (Tilesius, 1815). J. Shellfish Res. **14**: 173–177.

Zhou, S., and Shirley, T.C. 1996. Is handling responsible for the decline of the red king crab fishery? *In* High latitude crabs: biology, management, and economics. Alaska Sea Grant Rep. 96-02. pp. 591–612.

Appendix. Population model for Bristol Bay red king crab

The following model was applied to male crab. The female model is the same except that catch was replaced by handling mortality, and molting probability was set equal to 1.0. Abundances by length and shell condition in any one year result from abundances the previous year minus fishing, handling and natural mortality, plus recruitment and additions to or losses from each length-class due to growth:

$$\text{(A1)}\quad N_{l+1,\,t+1} = \sum_{l'=1}^{l'=l+1} \times [P_{l',\,l+1}\,((N_{l',t} + O_{l',t})\,e^{-M_t} - C_{l',t}\,e^{(y-1)M_t})\,m_{l'}] + R_{l+1,t+1}$$

$$O_{l+1,t+1} = ((N_{l+1,t} + O_{l+1,t})\,e^{-M_t} - C_{l+1,t}\,e^{(y-1)M_t}) \times (1 - m_{l+1})$$

where $N_{l,t}$ and $O_{l,t}$ are new- and old-shell crab abundances in length-class l and year t, M_t is instantaneous natural mortality in year t, m_l is molting probability, $R_{l,t}$ is recruitment, y is lag between abundance assessment and the fishery, and $P_{l',l}$ is the proportion of molting crab growing from length l' to length l after one molt. $C_{l',t}$ is catch (legal males) or handling mortality (sublegal males and females). Recruitment is defined as recruitment to the model and survey gear rather than recruitment to the fishery. $P_{l',l}$ and $R_{l,t}$ are computed as follows.

Mean growth increment per molt is assumed to be a linear function:

$$\text{(A2)}\quad G_l = a + b\iota$$

where a and b are constants. Growth increment per molt is assumed to follow a gamma distribution:

$$\text{(A3)}\quad g(x|\alpha_l, \beta) = x^{\alpha_l - 1} e^{-x/\beta} / (\beta^{\alpha_l} \Gamma(\alpha_l)).$$

The expected proportion of molting individuals growing from length-class l_1 to length-class l_2 after one molt is equal to the sum of probabilities with length range (ι_1, ι_2) of the receiving length class l_2 at the beginning of next year, i.e.,

$$\text{(A4)}\quad P_{l_1,l_2} = \int_{\iota_1 - \iota}^{\iota_2 - \iota} g(x|\alpha_l, \beta)\,dx$$

where ι is the midlength of length-class l_1.

Recruitment is separated into a time-dependent variable, R_t, and a length-dependent variable, U_l, representing the proportion of recruits belonging to each length-class:

$$\text{(A5)}\quad R_{l,t} = R_t U_l$$

where U_l is described by a gamma distribution similar to eqs. A3 and A4 with parameters α_r and β_r.

For each year, annual effective spawning biomass, SP_t, was estimated as

$$\text{(A6)}\quad SP_t = r_t \sum_l [F_{l,t} WF_l], \quad \iota \geq 90 \text{ mm CL}$$

where $F_{l,t}$ is female abundance in length-class l and year t, WF_l is mean weight of female crab in length-class l, ι is the midlength of length-class l, and r_t is the ratio of male reproductive potential MRP_t to total mature female abundance TMF_t (≥90 mm CL) in year t, i.e.,

$$\text{(A7)}\quad r_t = \begin{bmatrix} MRP_t / TMF_t, & \text{if } MRP_t < TMF_t \\ 1, & \text{if } MRP_t \geq TMF_t \end{bmatrix}$$

That is, if $r_t \geq 1$, then there are sufficient mature males to mate with all mature females, and so the number of spawning females is equal to the number of mature females. If $r_t < 1$, then not enough mature males are available to mate all mature females and the number of spawning females will be a fraction of mature females.

Male reproductive potential is defined as

$$\text{(A8)}\quad MRP_t = \sum_l [(N_{l,t} + O_{l,t}) mn_l], \quad \iota \geq 120 \text{ mm CL}$$

where $N_{l,t}$ and $O_{l,t}$ are mature male crab abundances in length-class l and year t with new- and old-shell conditions, respectively, and mn_l is the maximum number of females mated by a male in length-class l.

Annual recruitment is described by a general S–R model:

$$\text{(A9)}\quad R_t = SP_{t-k}^{r1} \quad e^{r2 - r3 SP_{t-k} + \upsilon_t}$$

where k is recruitment age, $r1$, $r2$, and $r3$ are constants, and environmental noise $\upsilon_t = \delta_t + a1\upsilon_{t-1}$. δ_t was assumed as a $N(0,\sigma)$.

Accuracy and precision in sampling hyporheic fauna

Brian G. Fraser and D. Dudley Williams

Abstract: A series of interstitial faunal samples was taken from a riffle in the Speed River, southern Ontario, Canada, to compare the field performance of four hyporheic samplers: the standpipe, colonization, and freeze corers and a pump sampler. Each of the samplers proved useful for collecting purely qualitative data, but statistical differences in some of the measured quantitative parameters were identified. The colonization corer significantly underestimated invertebrate density at each of the depths tested (20, 40, and 60 cm below the surface of the river bed). Taxonomic richness did not differ among the samplers. A sampling bias in the pump sampling method was identified in terms of both the proportion of insect larvae captured and the mean chironomid body size and is probably the result of a filtering effect of the interstices. Sampling precision estimates of density, richness, and organismal size ranged from 20 to 40%, but no pattern among the four samplers for any of the measures was observed. We conclude that, whereas the standpipe and freeze coring methods most effectively characterize the hyporheos, one of the other methods might prove acceptable under specific field circumstances or under certain practical constraints.

Résumé : Une série d'échantillons de la faune interstitielle a été prélevée dans un rapide de la rivière Speed, dans le sud de l'Ontario, Canada, pour comparer le rendement sur le terrain de quatre échantillonneurs hyporhéiques : la colonne montante, les carotteuses de colonization et avec congélation et un échantillonneur à pompe. Chacun des échantillonneurs s'est révélé utile pour prélever des données purement qualitatives, mais des différences statistiquement significatives ont été décelées dans le cas de certains des paramètres quantitatifs mesurés. La carotteuse de colonization a sous-estimé de manière significative la densité des invertébrés à chacune des profondeurs testées (20, 40 et 60 cm sous la surface du lit de la rivière). La richesse taxinomique n'a pas différé d'un échantillonneur à l'autre. Un biais d'échantillonnage a été observé dans le cas de l'échantillonneur à pompe en termes de proportion des larves d'insectes capturées et de taille moyenne des chironomidés capturées, et cette situation est sans doute attribuable à l'effet de filtration des interstices. La précision des estimations par échantillonnage de la densité, de la richesse et de la taille des organismes a varié entre 20 et 40 %, mais aucune tendance n'a été observée parmi les quatre échantillonneurs pour l'une ou l'autre des mesures effectuées. Nous concluons que si les méthodes de la colonne montante et du carottage avec congélation ont permis de caractériser le plus efficacement l'hyporhéos, une des autres méthodes pourrait se révéler acceptable dans des conditions particulières ou lorsqu'il faut respecter certaines contraintes pratiques.

[Traduit par la Rédaction]

Introduction

Recognition of the hyporheic zone (the interstitial habitat bordered by the surface water of a stream or river above and by true groundwater below) as an integral component of running waters has expanded the spatial extent of lotic ecosystems to include the vertical dimension (see Hynes 1980; Ward 1989). Yet, as hyporheic research progresses, it is prudent to acknowledge that a number of fundamental problems persist in obtaining accurate and precise quantitative and qualitative data on the hyporheos. Assessment of the relative collection efficiencies of different sampling devices, presently lacking, is essential if hyporheic research is to reach the experimental phase (Palmer 1993).

The numerous hyporheic sampling devices that have been used throughout the last few decades can be loosely assigned to four categories (Table 1). Although many of these designs have met with some success, no single sampler has been applied in all field situations, and there is disagreement as to which sampling techniques are most efficient (see reviews in Williams 1984 and Bretschko and Klemens 1986). In this study, we compared the field performance of hyporheic faunal samplers from each of the four categories. Specifically, for each sampler we assessed, at different sediment depths, accuracy and precision in terms of total invertebrate density, taxon richness, and invertebrate size distribution.

Study area

The Speed River, located in southern Ontario, flows through gently undulating hills, drumlin fields, glacial spillways, and swampy depressions (Chapman and Putnam 1966) with an average gradient of 2 m/km (Ontario Department of Planning and Development 1953). Approximately 80% of the watershed is used for mixed farming, although floodplains of the upper course are largely wooded, reforested, or maintained as rough pasture (Bishop and Hynes 1969). The main sampling area, the Rowan Farm study site (43°43′54″N, 80°16′24″W), ~5 km from the river's spring source, consists of a 40 m long riffle.

Received July 3, 1996. Accepted October 7, 1996.
J13536

B.G. Fraser[1] and D.D. Williams. Surface and Groundwater Ecology Group, University of Toronto at Scarborough, 1265 Military Trail, Scarborough, ON M1C 1A4, Canada.

[1] Author to whom all correspondence should be addressed. e-mail: bfraser@scar.utoronto.ca

Table 1. Summary of hyporheic sampler types.

Sampler type	Method of collection	References
(1) Nonfrozen sediment cores	Simultaneous extraction of interstitial water, sediments, and fauna	Williams and Hynes 1974, Palmer 1993
(2) Artificial substrates	Retrieval of device filled with representative or standard artificial substrate after suitable period of exposure to colonization by hyporheos	Hynes 1974, Boulton et al. 1991, Panek 1991
(3) Frozen sediment cores	Extraction of sediment core frozen to the outside of a standpipe following delivery of a coolant (e.g., liquid N_2, liquid CO_2)	Stocker and Williams 1972, Pugsley and Hynes 1983, Bretschko and Klemens 1986
(4) Pumps or bailers	Extraction of interstitial water and fauna from permanent or temporary standpipes or wells	Bou and Rouch 1967, Husmann 1971, Stanford and Ward 1988

River width varies from 4 to 6 m and water depth varies from 7 to 12 cm during baseflow conditions (mean weekly baseflow discharge approximately 3 m^3/s) to 70 cm or more at the height of spring runoff. To a depth of 30 cm, the substrate is composed primarily of gravels (<10 cm diameter) intermixed with silts and sands together with a few larger dolomite slabs. Below 30 cm, substrate heterogeneity is low and substrate composition is dominated by medium and fine sand (Stocker and Williams 1972).

Materials and methods

Between July 1 and July 21, 1994, six replicate samples from each of three depths (20, 40, and 60 cm below the surface of the river bed) were obtained at random locations along the length of the study riffle with each of four sampling devices: the standpipe corer (Williams and Hynes 1974); the freeze corer (after Stocker and Williams 1972); the colonization corer (Fraser et al. 1996); and a pump sampler (after Bou and Rouch 1967). All samples were preserved and stained in the field using a mixture of 10% formalin and Rose Bengal. In the laboratory, all samples were washed through a 53 μm mesh net and hand sorted under 10–40× magnification with the aid of a dissecting microscope. To facilitate comparison, all invertebrate densities were converted to and subsequently reported as standard densities per unit sediment volume (number of animals per litre sediment).

The colonization corer (Fig. 1) combines aspects of an artificial substrate sampler (after a prototype by Panek 1991) and a bundle piezometer (Cherry 1983) and is described in detail by Fraser et al. (1996). To sample fauna, sediment-filled acrylic colonization sleeves were inserted into the external standpipes. The sediment in the sleeves was mixed to specifications that mimicked the vertical sediment particle distribution of the river bed (obtained using the method of Stocker and Williams 1972). Following a colonization period of 9 weeks, the acrylic sleeves were removed from the corer with the aid of a tripod and winch. Both benthic (Mason et al. 1973; Lamberti and Resh 1985) and hyporheic (Coleman and Hynes 1970; Boulton et al. 1991) substrate colonization studies indicate that this is ample time for levels of both organic matter and fauna to return to natural levels. As the sleeves were withdrawn, they were wrapped in plastic film to prevent the loss of invertebrates. The sleeves were immediately cut into 20-cm sections (volume 125 mL) and the sediment from each section was transferred to plastic sample jars. Colonization corer samples included sediment ±10 cm from the depth indicated (e.g., the 20-cm sample ranged from 10 to 30 cm).

The standpipe corer (Fig. 1) (see Williams and Hynes 1974; Williams 1981) was driven into the river bed to the appropriate depth (20, 40, or 60 cm below the surface of the river bed) with a manual post driver. The corer was twisted clockwise until the inner sampling chamber was filled (volume 25 mL). The requisite number of turns needed to fill the chamber was determined by practice but was typically 7 to 10. Before removal, the chamber was locked in the closed position to prevent the loss of animals. Chamber contents were transferred to plastic sample jars. Standpipe corer samples included sediment ±5 cm from the depth indicated.

The freeze corer (Fig. 1) (see Stocker and Williams 1972; Bretschko and Klemens 1986) and two insulated copper rods were driven into the substratum with the post driver. Using a portable generator, an electric field (630 V, 60 Hz AC) was maintained for 10 min between the copper rods to paralyze the fauna. Bretschko and Klemens (1986) suggest that in situ electropositioning prevents animals from evading the cold front as the liquid nitrogen is delivered and is likely to keep the entire fauna immobilized for at least 15 min (Klemens 1983). After disconnecting the electrical field, a metal funnel was placed in the top of the standpipe and liquid nitrogen (8–10 kg) was delivered over a 10-min period. The frozen sediment core was extracted with the aid of a tripod and winch and then portioned into 10-cm segments. The dimensions of each section, along with its shape, were carefully recorded to accurately determine each section's volume. Frozen core sample volumes varied but generally comprised sediment ±10 cm from the depth indicated.

The pump sampler used (Fig. 1) was essentially the same as those designed by Husmann (1971) and Bou and Rouch (1967); however, an electric pump (rather than a manual pumping device) was used to facilitate sample collection. Replicate 1-L samples of interstitial material (water, fine-grained sediments, and organic matter) were obtained and subsequently transferred to plastic sample jars. The actual sediment volume from which the 1-L samples were collected was estimated based on previously determined porosity values of the sediment at this site (Stocker and Williams 1972).

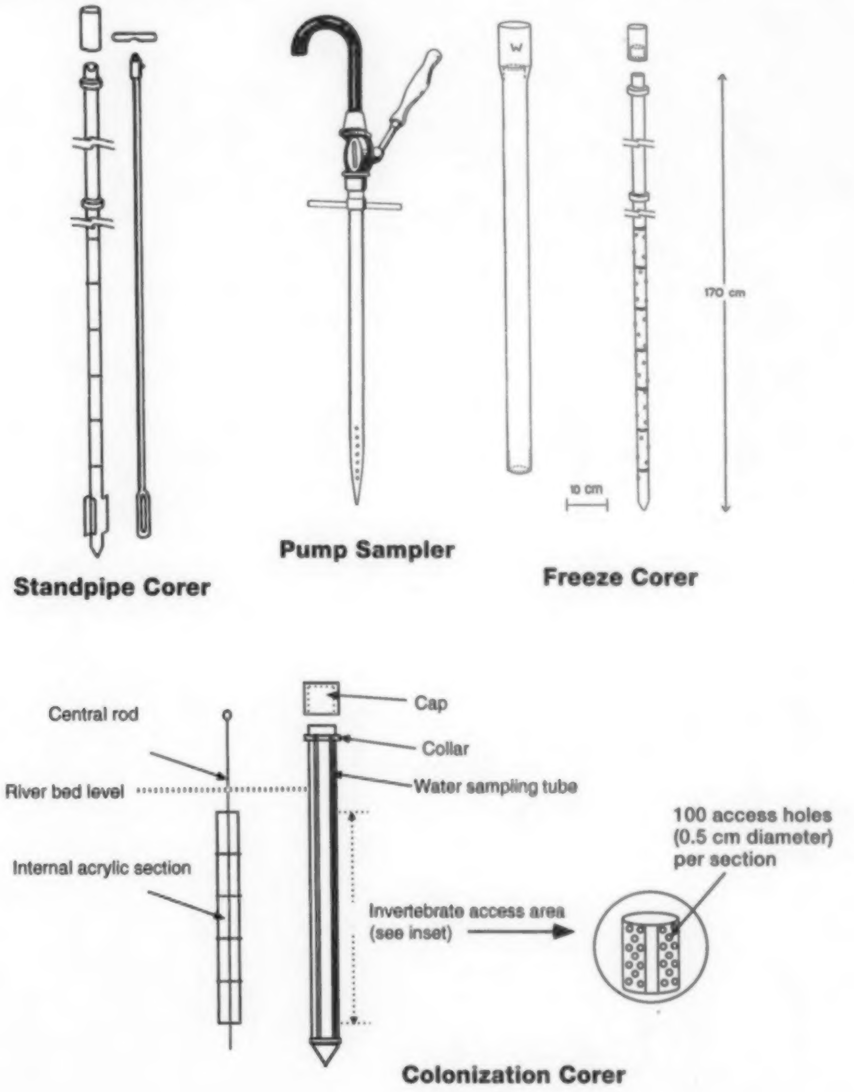
Numerical analyses

Density and taxonomic richness data were compared using a one-way ANOVA (SPSS Inc. 1995, version 6.1.3) to detect among sampling technique differences. A post-hoc Tukey-HSD test (SPSS Inc. 1995, version 6.1.3) was used to identify differences among individual treatments. Log-transformed density data were homoscedastic ($F_{\max}$; $P > 0.05$) and normally distributed (Wilk–Shapiro).

A comparison of the mean size (body length) of chironomid larvae (the most common taxon encountered) was performed using a one-way ANOVA and a post-hoc Tukey-HSD test to evaluate potential size–capture bias of any of the sampling methods. To facilitate this comparison, all chironomids captured were grouped according to both sampling technique and depth (nine groups in total). Body length (distance between the anterior of the head and the posterior of the last abdominal segment; Meyer 1989) was measured from a random subsample ($n = 25$) from each group. Individuals were selected with the aid of a random numbers table (Morris and Rolph 1981).

The effectiveness of the samplers at describing the hyporheic community at the Speed River was assessed in two ways. First, we qualitatively compared all of the taxa (at the gross taxonomic level, e.g., order) captured with each of the sampling methods. Secondly, the proportions of insect larvae obtained with each of the four samplers at each depth sampled were compared with a one-way ANOVA followed by a Tukey-HSD test. Proportion data were arcsine transformed to fulfil the assumptions of ANOVA.

Fig. 1. Diagrammatic representation of the four devices used to collect hyporheic samples: standpipe corer; freeze corer; colonization corer; and the pump sampler. Scale provided is approximate and applies to all samplers. The pump sampler used in this study is essentially the same as shown (after Husmann 1971), although unlike in the diagram, an electric pumping device was used to collect samples. W, weighted sleeve used for pounding the samplers into the stream bed.


W
170 cm
10 cm
Standpipe Corer
Pump Sampler
Freeze Corer
Central rod
Cap
Collar
River bed level
Water sampling tube
100 access holes
(0.5 cm diameter)
per section
Internal acrylic section
Invertebrate access area
(see inset)
Colonization Corer

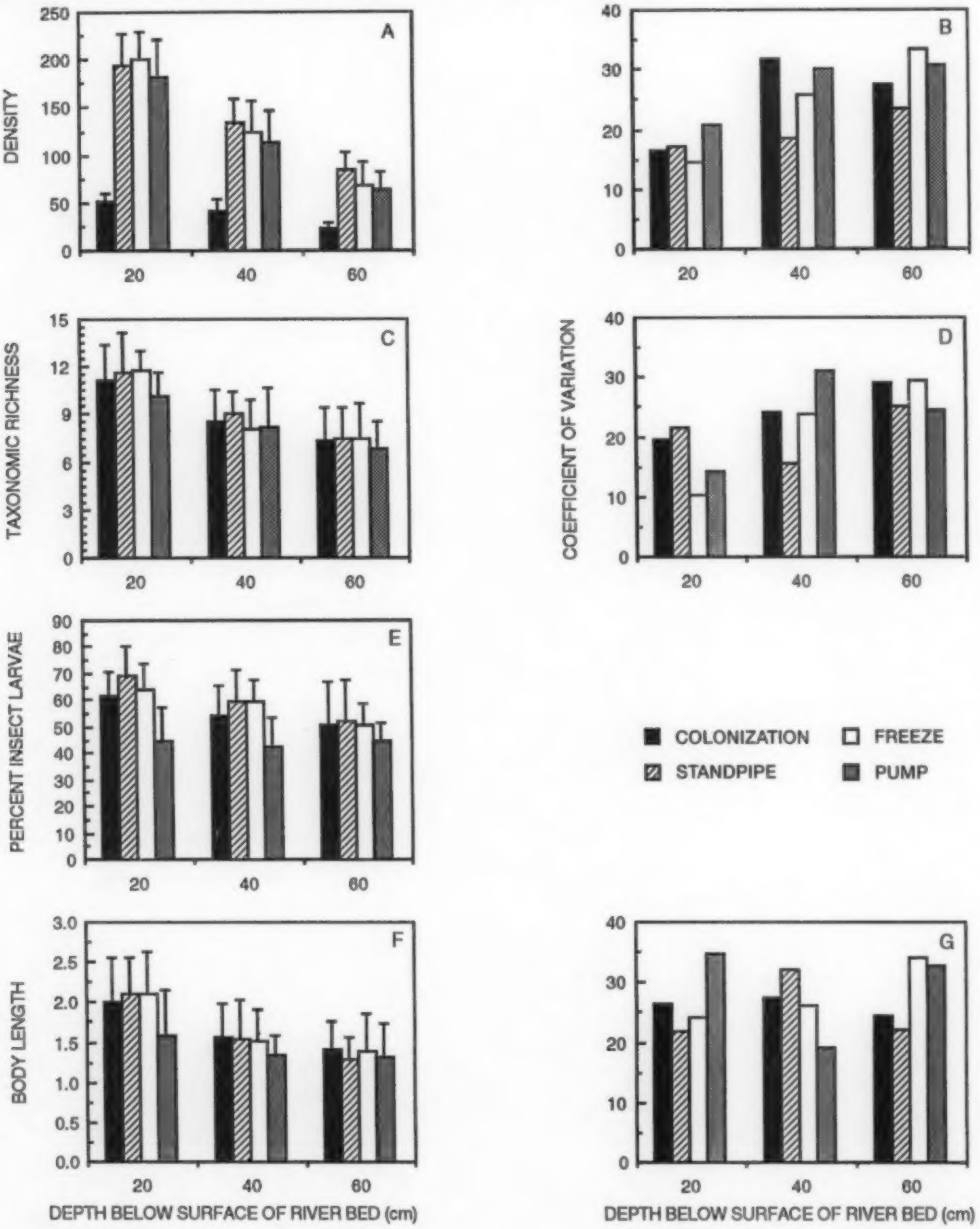
The coefficient of variation (CV; standard deviation expressed as the percentage of the mean; Sokal and Rohlf 1981) was used to measure precision among the four sampling devices for the density, taxon richness, and chironomid size data.

Separate studies using the standpipe corer (Williams 1981) and the freeze corer following in situ electropositioning (Bretschko 1985; Bretschko and Klemens 1986) concluded that each of the methods provided accurate quantitative estimates of hyporheic community structure (e.g., density). We therefore made the a priori assumption that the numbers derived from these methods (i.e., density, taxon richness, size, and community measures) would be the accuracy standard with which the colonization corer and pump sampler would be compared.

Results

A significant difference was detected among density estimates derived with the four samplers at each of the three depths tested (Fig. 2A, Table 2). In each case, the Tukey-HSD test identified only the colonization corer estimates as different ($P < 0.05$) from those obtained with the other methods. In general, greater than 40–50% of all animals captured were found at a depth of 20 cm. This pattern was evident for each of the samplers and has been noted both at this site (e.g., Williams and Hynes 1974; Godbout and Hynes 1982) and others (e.g., Williams 1989; Bretschko 1992). Total density estimates for the standpipe and

Fig. 2. Comparison of hyporheic faunal samples at three depths taken with four devices at the Speed River: (A) invertebrate density (number of animals per litre of substrate) and (B) its coefficient of variation (CV; %); (C) taxonomic richness (gross taxonomic level) and (D) its CV; (E) proportion of insect larvae captured (%); and (F) mean chironomid size (mm) and (G) its CV.



freeze corers and the pump sampler were similar to those reported previously at this site during the same time of year (Williams and Hynes 1974; Fraser 1995).

The potential capture bias of any of the hyporheic samplers for a particular taxon or group of taxa was determined by comparing mean richness among the samplers at the three test depths (Fig. 2C). No differences in taxonomic richness among the samplers were detected (Table 2). Richness was greatest at 20 cm and decreased with increasing depth; the same pattern was evident with each of the samplers tested.

Taxonomic capture bias was assessed also by comparing qualitative and quantitative aspects of hyporheic community structure. Qualitatively, all of the samplers captured individuals from greater than 90% of the same taxa. All samplers captured individuals from the Nematoda, Mollusca, Ostracoda, Copepoda, Acari, Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, and Diptera. However, Tardigrada were captured only with the freeze and pump samplers; Cladocera with the standpipe, colonization, and pump samplers; and Amphipoda with the standpipe, colonization, and freeze samplers. For a quantitative analysis, the proportion of larvae of all insect taxa present in samples obtained with each of the samplers for the three depths was compared (Fig. 2E). Only at a depth of 20 cm was a difference among samplers detected ($P < 0.05$). The proportion of insect larvae obtained with the pump sampler was different from the other three methods (Tukey-HSD test, $P < 0.05$). Although no significant differences were detected at depths of 40 or 60 cm, the proportion of insect larvae obtained with the pump sampler was generally less than that obtained with either the standpipe, colonization, or freeze corers.

Chironomid body size decreased with increasing depth for all of the samplers, although to a lesser extent for the pump sampler (Fig. 2F). A significant difference in size was detected among the samplers at a depth of 20 cm (Table 2) with the pump sampler collecting smaller larvae than the other three methods (Tukey-HSD test).

For all of the samplers tested and all of the measures compared (density, richness and size), the CV was generally between 20 and 40% and increased with depth (Figs. 2B, 2D, and 2G). No pattern was obvious among samplers, and none had consistently high CV values across all of the measures evaluated nor for any of the measures individually.

Table 2. One-way ANOVA summaries for density, richness, size, and hyporheic community structure (proportion of insect larvae) comparisons among the four sampling methods at each of the three test depths.

Measure	Depth	*F*	*P*
Density	20	28.9044	<0.0001
	40	12.2996	0.0001
	60	10.1102	0.0003
Taxonomic richness	20	0.7685	0.5251
	40	0.2373	0.8693
	60	0.1255	0.9439
Chironomid size	20	5.2686	0.0021
	40	1.6674	0.1792
	60	0.7409	0.5303
Proportion of insect larvae captured	20	4.5807	0.0134
	40	2.8676	0.0622
	60	0.3740	0.7727

Discussion

Accuracy and precision

In a strict sense, only with sampling devices that remove an exact, representative portion of habitat is it possible to obtain absolute measures. Of the four samplers tested, only the freeze corer meets this criterion. Previous field and laboratory tests of the accuracy of the freeze coring technique, following in situ positioning, have concluded that the device provides accurate quantitative measures (Pugsley and Hynes 1983; Bretschko 1985; Bretschko and Klemens 1986). To our knowledge of the four sampler types tested in this study, only the standpipe corer has been previously evaluated quantitatively. Williams (1981) compared density estimates and the range of taxa captured with the standpipe corer to similar measures from buckets of substrate from which the cores were taken. The corer produced a mean error estimate of total numbers of only 19%, and virtually all of the most common taxa in the substrates sampled were captured. Both Elliott (1977) and Cummins (1975) suggest that this level of accuracy is acceptable in estimating benthic densities, and perhaps the same is applicable to the hyporheos.

Given the conclusions of these previous tests, we initially assumed that both the freeze and standpipe corers would provide accurate estimates for the variety of parameters we measured. No statistical differences were detected between the freeze and standpipe corers for any of the measured variables at any of the three test depths. As it is unlikely that both devices would exhibit the same capture bias in each case we believe that our a priori assumption was a reasonable one.

All four of the samplers tested would suffice for collecting purely qualitative (e.g., species list) data; however, this is not the case for quantitative measures. The colonization corer consistently underestimated total invertebrate density. We suggest that this could be a result of loss of animals upon retrieval of the inner, substrate-filled acrylic sleeves. Alternatively, it is possible that the introduced substrate lacked the particle packing, arrangement, and (or) organic matter content of the natural interstitial sediments and therefore was colonized by a novel invertebrate community. Whereas there has been extensive work done on the colonization of artificial benthic substrates (see review in Rosenberg and Resh 1982), to date little is known about the physical habitat requirements of the hyporheos. It may be that the information presently available regarding the colonization of sediments may be inaccurate for hyporheic substrate colonization samplers. More investigation of subsurface colonization dynamics therefore is clearly required.

The pump sampler we tested was capture selective in terms of both insect larvae and organism size. This bias was most conspicuous at a depth of 20 cm, coincidentally the depth at which the largest proportion of insect larvae and the biggest animals (i.e., near-emergence late-instar individuals) were found. We suggest that this bias is the result of a filtering effect of the interstices. Larger animals and animals with a body morphology that make it possible for them to grasp on to substrate particles are likely to resist the suction of the pump and are therefore likely to be underrepresented during sampling.

High levels of precision in the data would be desirable, for example, in manipulative studies where some control condition is compared with an experimental treatment. In this situation it would be advantageous to use a sampling device that had a reliably high level of precision for the measure of interest. None of our samplers outperformed the others for all measures or for any measure individually, with respect to precision. It would appear, therefore, that any one of the samplers would be equally appropriate to generate an acceptable level of precision.

Comments on the performance and applicability of hyporheic fauna samplers

Despite their similar qualitative performance, it is unlikely that any one device would be useful in all field situations or for all purposes. For example, the freeze core method can provide a useful description of the invertebrates and substrate especially when escape of invertebrates in response to physical disturbance or temperature gradients has been minimized by in situ positioning. Yet, in certain situations, it may not be a practical or appropriate technique. Removing a series of frozen cores from a stream bed destroys the habitat for an undetermined, but extended, period. Although the disturbed sediments would be recolonized and organic matter levels would probably return to normal conditions, the potentially permanent alteration of interstitial flow dynamics and vertical sediment and interstitial pore space configurations may render the freeze corer unsuitable for monitoring localized temporal patterns or for experimental work. As these two research areas appear to be the focus of present and future hyporheic studies (Palmer 1993; Jones and Holmes 1996), it is likely that the applicability of freeze corers may now be somewhat limited, especially as there are numerous logistical constraints that hinder their use including (*i*) the equipment is heavy and cumbersome; (*ii*) retrieval of the core can be an arduous task, especially for samples taken deep in the bed; and (*iii*) freeze coring will not work well in a river with buried boulders. (In fact, none of the devices works well in rivers with buried boulders as they all initially require some degree of manual insertion into the bed.)

Advantages and disadvantages associated with the use of the colonization corer are probably similar to those common to all artificial substrates used to sample freshwater benthic macroinvertebrates (see review by Rosenberg and Resh 1982). Possible problems include (*i*) a loss of information on natural variation in the spatial distribution of animals (Rosenberg and Resh 1982), although this can be addressed by filling the acrylic sleeves with simulated natural mixtures of sediment; (*ii*) a potential capture bias for particularly active taxa because artificial substrates largely measure the relative activity of taxa within the community, although no evidence of this was noted with the colonization corer (activity of the hyporheos may be related to ambient temperatures and therefore there may be a seasonal component to the selection bias); and (*iii*) the underestimate of total animal density probably as a result of the loss of animals during substrate retrieval. To remedy this latter problem Coleman and Hynes (1970) used a mesh bag in between the outer and inner sediment-filled pots buried in the stream bed to capture animals that would have been otherwise lost during retrieval. This was not incorporated into the design of the colonization corer because we thought it more prudent to have as small a space as possible (<3 mm) rather than having a large gap between the inner and outer portions (as in the case with the Coleman and Hynes device). A large gap between the natural and artificial substrates has the potential to create novel access routes for the movement of both interstitial organisms and water.

However, the colonization corer also has a number of advantages. Firstly, once the outer steel standpipes have been installed in the bed, sampling be can completed with minimum habitat disturbance. Secondly, substrate characteristics (e.g., vertical sediment profile, organic matter quantity or quality, standardized vs. representative substrate) can be manipulated to investigate hyporheic colonization dynamics. The ability to control or mimic substrate characteristics makes the colonization corer useful for sampling a wide range of substrate types. Thirdly, the design of the colonization corer makes it possible to collect not only faunal samples, but also the water sampling tubes fixed to the outer standpipe permit continuous monitoring of the hydrogeological and chemical features of the system. The colonization corer, therefore, has the potential to be an effective hyporheic sampling device, especially for experimental manipulations in the field.

The standpipe corer was effective for characterizing all aspects of the hyporheic community: it is a versatile sampler that provides instantaneous samples with minimum disturbance and can be easily modified to collect interstitial water. The two most obvious disadvantages to the standpipe corer are both mechanical: (*i*) it is very labour intensive in that it may take up to several minutes of continuous sledge hammering to insert the standpipe into deeper parts of the bed; and (*ii*) any large substrate particles, and probably their associated fauna, will not be sampled.

Although pump samplers have been and are currently being used extensively in hyporheic studies, our data indicated that all types of insect larvae and particularly late-instar chironomids, were underrepresented in samples obtained with this technique. Pump samplers are not without some merit, for example, they can be permanently installed to facilitate continuous monitoring with minimal physical effort and long-term habitat disturbance. Permanently installed standpipes or wells can be used also as piezometers and, therefore, can facilitate collection of hydrogeologic and (or) water chemistry data.

We conclude that the ideal hyporheic sampler still evades researchers and indeed may not be attainable. Nevertheless, within the range of samplers examined in this study, protocols exist that allow acceptable levels of sediment description, water sampling and faunal characterization to be made, although not through one apparatus alone.

Acknowledgements

We are grateful to the landowners, the MacKenzie family, for not only providing us with unlimited access to the field site, but also for their interest in our work. We thank Allan Wong and Marilyn Smith for help with the field work and Drs. Nancy Williams and Ian Hogg for useful comments on the manuscript. Dr. Maurice Lock contributed both brain and muscle power to sampling design in "the early years." This project was funded by a grant from the Natural Sciences and Engineering Research Council of Canada to D.D.W.

References

Bishop, J.E., and Hynes, H.B.N. 1969. Upstream movements of the benthic invertebrates in the Speed River, Ontario. J. Fish. Res. Board Can. **26**: 279–298.

Bou, C., and Rouch, R. 1967. Un nouveau champ de researches sur la faune aquatique souterraine. C. R. Hebd. Séances Acad. Sci. Ser. III, **265**: 369–370.

Boulton, A.J., Stibbe, S.E., Grimm N.B., and Fisher, S.G. 1991. Invertebrate recolonization of small patches of defaunated hyporheic sediments in a Sonoran Desert stream. Freshwater Biol. **26**: 267–277.

Bretschko, G. 1985. Quantitative sampling of the fauna of gravel streams. Verh. Int. Ver. Theor. Angew. Limnol. **22**: 2949–2052.

Bretschko, G. 1992. Differentiation between epigeic and hypogeic fauna in gravel streams. Regul. Rivers Res. Manage. **7**: 17–22.

Bretschko, G., and Klemens, W.E. 1986. Quantitative methods and aspects in the study of the interstitial fauna of running waters. Stygologia, **2**: 297–316.

Chapman, L.J., and Putnam, D.F. 1966. The physiography of southern Ontario. University of Toronto Press, Toronto, Ont.

Cherry, J.A. 1983. Piezometers and other permanently installed devices for groundwater monitoring. *In* Proceedings of the Petroleum Association for Conservation of the Canadian Environment, May 2–5, 1982, Ottawa, Ont. Petroleum Association for Conservation of the Canadian Environment, Ottawa, Ont. pp. IV1–IV39.

Coleman, M.J., and Hynes, H.B.N. 1970. The vertical distribution of the invertebrate fauna in the bed of a stream. Limnol. Oceanogr. **15**: 31–40.

Cummins, K.W. 1975. Macroinvertebrates. *In* River ecology. *Edited by* B.A. Whitton. University of California Press, Berkeley, Calif. pp. 170–199.

Elliott, J.M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Sci. Publ. No. 25. 2nd ed. Freshwater Biological Association, Ambleside, U.K.

Fraser, B.G. 1995. Boundary flux of the hyporheic zone as determined by biotic and abiotic factors. M.Sc. thesis, University of Toronto, Toronto, Ont.

Fraser, B.G., Williams, D.D., and Howard, K.W.F. 1996. Monitoring biotic and abiotic processes across the hyporheic/groundwater interface. Hydrogeol. J. **4**: 36–50.

Godbout, L., and Hynes, H.B.N. 1982. The three dimensional distribution of the fauna in a single riffle in a stream in Ontario. Hydrobiologia, **97**: 87–96.

Husmann, S. 1971. Eine neue Methode zur Entnahme von Interstitialwasser aus subaquatischen Lockergesteinen. Arch. Hydrobiol. **68**: 519–527.

Hynes, H.B.N. 1980. Groundwater and stream ecology. Hydrobiologia, **100**: 93–99.

Jones, J.B., Jr. and Holmes, R.M. 1996. Surface–subsurface interactions in stream ecosystems. Trends Ecol. Evol. **11**: 239–242.

Klemens, W. 1983. Zur problematik quantitativer probennahmen in bettsedimenten von Schotterbachen. Jahresberieht Biologische Station Lunz, Austria, **6**: 25–47.

Lamberti, G.A., and Resh, V.H. 1985. Comparability of introduced tiles and natural substrates for sampling lotic bacteria, algae and macroinvertebrates. Freshwater Biol. **15**: 21–30.

Mason, W.T., Jr., Weber, C.I., Lewis, P.A., and Julian, E.C. 1973. Factors affecting the performance of basket and multiplate macroinvertebrate samplers. Freshwater Biol. **3**: 409–436.

Meyer, E. 1989. The relationship between body length parameters and dry mass in running water invertebrates. Arch. Hydrobiol. **17**: 191–203.

Morris, C.N., and Rolph, J.E. 1981. Introduction to data analysis and statistical inference. Prentice-Hall, Inc. Englewood Cliffs, N.J.

Ontario Department of Planning and Development. 1953. Speed Valley Conservation Report. Ontario Department of Planning and Development, Toronto, Ont.

Palmer, M.A. 1993. Experimentation in the hyporheic zone: challenges and prospectus. J. North Am. Benthol. Soc. **12**: 84–93.

Panek, K.L.J. 1991. Migrations of the macrozoobenthos within the bedsediments of a gravel stream (Ritrodat–Lunz study area, Austria). Verh. Int. Ver. Theor. Angew. Limnol. **24**: 1944–1947.

Pugsley, C.W., and Hynes, H.B.N. 1983. A modified freeze-core technique to quantify the distribution of fauna in stony streambeds. Can. J. Fish Aquat. Sci. **40**: 637–643.

Rosenberg, D.A., and Resh, V.H. 1982. The use of artificial substrates in the study of freshwater benthic macroinvertebrates. *In* Artificial substrates. *Edited by* J. Cairns. Ann Arbor Science Publishers, Inc., Ann Arbor, Mich. pp. 175–235.

Sokal, R.R., and Rohlf, F.J. 1981. Biometry. 2nd ed. W.H. Freeman & Co., New York.

SPSS Inc. 1995. SPSS® for Windows™. Base system user's guide, release 6.0. SPSS Inc., Chicago, Ill.

Stocker, Z.S.J., and Williams, D.D. 1972. A freezing core method for describing the vertical distribution of sediments in a stream bed. Limnol. Oceanogr. **17**: 136–139.

Ward, J.V. 1989. The four-dimensional nature of lotic ecosystems. J. North Am. Benthol. Soc. **8**: 2–8.

Williams, D.D. 1981. Evaluation of a standpipe corer for sampling aquatic interstitial biotopes. Hydrobiologia, **83**: 257–260.

Williams, D.D. 1984. The hyporheic zone as a habitat for aquatic insects and associated arthropods. *In* The ecology of aquatic insects. *Edited by* V.H. Resh and D.M. Rosenberg. Praeger Publishers, New York. pp. 430–455.

Williams, D.D. 1989. Towards a biological and chemical definition of the hyporheic zone in two Canadian rivers. Freshwater Biol. **22**: 189–208.

Williams, D.D., and Hynes, H.B.N. 1974. The occurrence of benthos deep in the substratum of a stream. Freshwater Biol. **4**: 233–256.

Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}N$) and literature dietary data

M. Jake Vander Zanden, Gilbert Cabana, and Joseph B. Rasmussen

Abstract: Stable nitrogen isotope ratios ($\delta^{15}N$) are commonly used to represent the trophic structure of aquatic systems, yet the ability of $\delta^{15}N$ to indicate the trophic position of aquatic consumers remains untested using traditional dietary methods. Interpreting the $\delta^{15}N$ of aquatic consumers relative to large, long-lived primary consumers such as unionid mussels provides a continuous measure of an organism's trophic position that adjusts for among-system variation in baseline $\delta^{15}N$. We used this method to estimate the trophic position of eight littoral fish species from 36 lakes in Ontario and Quebec. We validated these $\delta^{15}N$ measures of trophic position by compiling literature dietary data from 342 populations of these same fish species and calculated a continuous measure of trophic position for each population. Mean dietary trophic position estimates corresponded closely to ^{15}N estimates, with mean trophic position ranging from 3.3 for pumpkinseed (*Lepomis gobbosus*) to 4.4 for walleye (*Stizostedion vitreum*). Both methods indicated approximately one trophic level of variation among populations of a species. This study confirms the ability of baseline-adjusted $\delta^{15}N$ to represent the trophic position of aquatic consumers.

Résumé : Les rapports d'un isotope stable de l'azote ($\delta^{15}N$) sont couramment utilisés pour représenter la structure trophique des systèmes aquatiques; pourtant, la capacité du $\delta^{15}N$ d'indiquer la position trophique des consommateurs aquatiques n'a pas encore été testée employant des méthodes alimentaires traditionnels. L'interprétation de $\delta^{15}N$ des consommateurs aquatiques par rapport aux consommateurs primaires de grande taille et de longue durée de vie comme les moules de la famille des unionidés fournit une mesure continue de la position trophique d'un organisme qui s'ajuste pour tenir compte de la variation intersystèmes de $\delta^{15}N$ de base. Nous avons utilisé cette méthode pour estimer la position trophique de huit espèces de poissons littoraux dans 36 lacs du Québec et de l'Ontario. Nous avons validé ces mesures de position trophique par $\delta^{15}N$ en rassemblant, dans la documentation scientifique, les données sur le régime alimentaire de 342 populations de ces mêmes espèces de poisson et avons calculé une mesure continue de la position trophique de chacune de ces populations. La valeurs estimées de la position trophique alimentaire moyenne correspondaient étroitement aux valeurs estimées de ^{15}N, la position trophique moyenne variant de 3,3 pour le crapet-soleil (*Lepomis gobbosus*) à 4,4 pour le doré jaune (*Stizostedion vitreum*). Les deux méthodes ont indiqué une variation d'environ un niveau trophique entre les populations d'une même espèce. Cette étude confirme la capacité du $\delta^{15}N$ ajusté en fonction de la ligne de base de représenter la position trophique des consommateurs aquatiques.

[Traduit par la Rédaction]

Introduction

Accurate representation and description of trophic relationships are essential to a wide range of ecological studies. The concept of discrete trophic levels is commonly used in ecological studies and has been used successfully in studies predicting contaminant bioaccumulation in top predators (Rasmussen et al. 1990; Cabana et al. 1994). Furthermore, trophic levels provide the framework for studies of cascading trophic interactions (Carpenter et al. 1985; Wooton and Power 1993) and ecological energetics and efficiencies (Lindeman 1942; Kerr and Martin 1970). The food chain approach contrasts with food web studies, which focus on the complexity of trophic relationships in nature (Sprules and Bowerman 1988). Although food web studies recognize and quantify important attributes such as omnivory, cannibalism, and reciprocal predation (Sprules and Bowerman 1988; Polis 1991), designation of "trophic linkages" is a subjective process that fails to consider the energetic importance of the represented trophic connections (Paine 1988).

Food chains and food webs represent extreme endpoints of models used to represent trophic relationships; both approaches have the potential to misrepresent the pathways of mass transfer and energy flow through ecosystems (Murdoch 1966; Kling et al. 1992; Vander Zanden and Rasmussen 1996). Use of a continuous measure of trophic position (analogous to the concept of "realized" trophic structure of Kling et al. (1992)) provides energetically based representations of trophic relationships (Levine 1980). Trophic position calculations weigh trophic connections according to their relative energetic importance, thereby serving as a compromise between discrete food chain and food web models (Vander Zanden and Rasmussen 1996). This general approach has been successfully applied to modelling of mercury (Cabana and Rasmussen

Received April 9, 1996. Accepted October 7, 1996.
J13395

M.J. Vander Zanden,[1] G. Cabana,[2] and J.B. Rasmussen. Department of Biology, McGill University, 1205 Ave. Docteur Penfield, Montreal, QC H3A 1B1, Canada.

[1] Author to whom all correspondence should be addressed. e-mail: jzanden@bio1.lan.mcgill.ca

[2] Present address: Department of Integrative Biology, University of California at Berkley, Berkley, CA 94720, U.S.A.

1994) and polychlorinated biphenyls (Vander Zanden and Rasmussen 1996) bioaccumulation in aquatic food webs.

A continuous measure of an organism's trophic position can be obtained in two ways. The dietary approach uses estimates of the trophic position of prey organisms and volumetric stomach content data, preferably for large numbers of fish. Weighted averages are then used to calculate a continuous measure of the population's trophic position (Winemiller 1990; Vander Zanden and Rasmussen 1996). A second approach relies on the consistent enrichment of the stable nitrogen isotope, ^{15}N (3.4 ± 0.3‰) between prey and predator (Minagawa and Wada 1984; Owens 1987; Peterson and Fry 1987; Cabana and Rasmussen 1994), allowing its use as a measure of an organism's trophic position that accounts for omnivory (Cabana and Rasmussen 1994). Previous comparative stable isotope – food web studies have been complicated by among-system variation in the ^{15}N signatures characterizing primary producers at the base of the food web. Cabana and Rasmussen (1996) overcame this problem by measuring an organism's ^{15}N ratios ($\delta^{15}N$) relative to the lake-specific $\delta^{15}N$ signature of commonly occurring primary consumers such as unionid mussels. This provides a continuous measure of an organism's trophic position amenable to comparative, multisystem studies of trophic structure.

The objective of this study was to verify $\delta^{15}N$ as a measure of trophic position for a series of littoral freshwater fish species. We calculated the trophic position of eight species of freshwater fish using dietary data and ^{15}N and compared the mean and variation in trophic position estimates attained using the two techniques. Previous studies have attempted to verify the $\delta^{15}N$ measure of trophic position using within-system comparisons between dietary data and $\delta^{15}N$ (Wainright et al. 1993) and attributed discrepancies to the inability of dietary data to represent temporal variation in feeding and errors in trophic position estimates of prey items. Our comparison differs in that it relies on dietary trophic position estimates for 342 fish populations and $\delta^{15}N$ estimates from 113 fish populations from 36 lakes. Although the actual fish populations for our two methods do not overlap, the large sample sizes provide a robust comparison of these two measures of trophic position and serve as a test of the $\delta^{15}N$ measure of trophic position recently proposed by Cabana and Rasmussen (1996).

Materials and methods

Dietary analysis and trophic position calculations

Dietary data for adults of eight common eastern North American game fish species were collected from literature sources: northern pike (*Esox lucius*), chain pickerel (*Esox niger*), rock bass (*Ambloplites rupestris*), pumpkinseed (*Lepomis gibbosus*), smallmouth bass (*Micropterus dolomieu*), largemouth bass (*Micropterus salmoides*), yellow perch (*Perca flavescens*), and walleye (*Stizostedion vitreum*). Data for northern pike and chain pickerel were pooled due to the small number of lakes with chain pickerel and the similar ecology, morphology, and feeding behavior of these species (Scott and Crossman 1973). These eight species were chosen because of the abundance of dietary data in the literature and because we have stable isotope estimates of trophic position for these same species from a large number of lakes.

Although the degree of taxonomic detail of prey categories in the published studies was highly variable, it was usually possible to separate prey items into the following categories: fish, zooplankton, omnivorous zoobenthos, predatory zoobenthos, mollusks, crayfish, detritus/plants/debris, and others (includes mammals, birds, and amphibians and unidentified materials). For the two highly piscivorous species, northern pike and walleye, the fish component was further subdivided to species where data permitted.

Diet data expressed as the percent contribution of a prey item to total gut volume were used for this study (also reported as percentage of dry or wet weight). Data reported in the "percentage of total number of prey organisms" format were converted to percentage of total volume using prey weight values from the dietary study, or mean values from literature reports of invertebrate prey weight (Cummins and Wuycheck 1971; Driver et al. 1974; Smock 1980; Lawrence et al. 1987). Data expressed as "percent frequency of occurrence" were not utilized in this study due to the potential error accompanying conversion of dietary data into a volumetric format.

When data for adult and juvenile fish were reported separately, only adult fish were retained for analysis; division of data in the published sources according to fish size, age, month, season, depth, and time of day was averaged for each year and treated as a single observation. When possible, data for multiple years from a lake were treated as separate observations, as a year roughly corresponds to the period of time for which an adult fish's diet is integrated using ^{15}N (Hesslein et al. 1993). The fish dietary data set contained 342 lake–year observations for a total of 65 987 individual fish. The average diet (percent volumetric contribution of each of the previously mentioned prey categories) was calculated for each fish species.

Calculation of "trophic position" of a fish population required estimating the trophic position of prey organisms. We define primary producers as trophic level "1", primary consumers as trophic level "2", and so on. Since specific trophic interactions among invertebrate organisms remain poorly understood, the simplest possible assumptions concerning the trophic position of prey were used in this study (Table 1). Prey items known to be predominantly predatory were assigned values of 3.0; strictly herbivorous prey were assigned values of 2.0. Prey items known to be omnivorous, such as zooplankton and most orders of aquatic insect larvae, were assigned an intermediate trophic position value of 2.5, for lack of information about their realized trophic position. For piscivorous fish, northern pike and walleye, trophic position was calculated in two ways. One used all the available dietary data and assigned all fish prey items to trophic level 3.5. The second approach used only data where the fish components of their diets were further broken down to species.

Clearly, a limitation of this dietary approach is that we must assume and simplify trophic interactions at lower levels of the food web. Although the trophic positions of prey items do vary within systems and through time, our large sample sizes would cause any errors associated with these assumptions to remain constant among the fish species included in this study. Following Winemiller (1990) and Vander Zanden and Rasmussen (1996), the fish dietary data from each lake and the trophic position estimates for prey items were used to calculate trophic position for each fish population using the formula

$$T_a = \Sigma(V_i \cdot T_i) + 1 \quad (1)$$

where T_a = mean trophic position of the ath predator population, V_i = volumetric contribution of the ith prey item, and T_i = trophic position of the ith food item. Although prey items may have been represented by discrete trophic level estimates, this weighted average calculation generates a continuous, fractional measure of trophic position for each fish population. The large number of populations included in this study permits a reliable estimate of the average trophic position for each species, as well as the degree of among-system variability in trophic position for each species.

^{15}N calculation of trophic position

Adult individuals of these eight fish species were collected from 36 lakes (113 fish populations) in Ontario and Quebec and were analyzed for $\delta^{15}N$ using a Europa Tracermass mass spectrometer (Cabana and

Table 1. Estimated trophic position values for prey items used in dietary calculations of trophic position.

Prey category	Estimated trophic position	Includes
Fish	2.5	Cyprinids
	3.0	Alewife[a]
	3.2	Whitefish,[a] cisco[a]
	3.3	Centrarchids
	3.5	Suckers, trout, burbot, white bass, unidentified fish, others
	3.7	Yellow perch, trout-perch,[a] stickleback,[a] smelt,[a] sculpins[a]
Zooplankton	2.5	Cladocera, Copepoda, Ostracoda, Rotifera
Omnivorous zoobenthos	2.5	Tricoptera, Ephemeroptera, Plecoptera, Hemiptera, Coleoptera, Diptera, Oligochaeta, Amphipoda (*Gammarus* sp., *Hyalella* sp., *Diporia hoyi*, *Mysis relicta*), other unidentified insect larvae and benthic invertebrates
Predatory zoobenthos	3.0	Odonata, Hirudinea, Megaloptera
Molluscs	2.0	Gastropoda, Pelecypoda
Crayfish	3.0	Decapoda
Detritus	1.0	Detritus, plants, mud
Other	2.5	Amphibians, mammals, waterfowl, unidentified materials

[a] Trophic position estimated using dietary data (from Vander Zanden and Rasmussen 1996).

Rasmussen 1996). These N isotopic values alone cannot be considered to represent trophic position, since the $\delta^{15}N$ of primary producers (defined as organisms that convert inorganic N to organic N) are highly variable among systems (Kling et al. 1992; Kline et al. 1993; Cabana and Rasmussen 1996) and within systems through time (Toda and Wada 1990; Gu et al. 1994; Cabana and Rasmussen 1996). This necessitates that the isotopic signature of fish be measured relative to a lake-specific "baseline" $\delta^{15}N$ signature. Cabana and Rasmussen (1996) interpreted fish $\delta^{15}N$ relative to unionid mussels. These relatively large and long-lived primary consumer organisms integrate temporal variability in primary producer $\delta^{15}N$, thereby representing the average baseline $\delta^{15}N$ signature. Unionid mussel $\delta^{15}N$ (n = 1–9 mussels per lake) were measured for each of the 36 study lakes. A continuous measure of trophic position (corresponding to the dietary estimates of trophic position) was calculated for each fish population using the formula

$$(2)\qquad \text{Trophic position} = [(\text{fish } \delta^{15}N - \text{mussel } \delta^{15}N)/3.4] + 2$$

where 3.4 represents a 1.0 trophic level increment in $\delta^{15}N$.

Results

Dietary estimates of trophic position

The raw dietary data compiled for this study are presented in Appendix I. These data were summarized by calculating the average diet (percentage of total stomach volume ± 1 SD) for each species (Table 2). The summary results of the average diets of these fish are generally consistent with previous reports of the diets characterizing these species. Nearly 40% of the average diet of pumpkinseed consisted of mollusks. Fifty-three percent of yellow perch prey consisted of zoobenthos, of which more than 10% were identified as amphipods. Rock bass consumed 42% benthic invertebrates and 32% crayfish. The diet of smallmouth bass consisted of 37% fish, 28% zoobenthos, and 28% crayfish. Fifty percent of the average diet of largemouth bass consisted of fish prey. Both northern pike and walleye consumed about 85% fish. More detailed analysis of the fish components of the diets of northern pike and walleye (Appendix II) shows that walleye consume 29% yellow perch and only 8% cyprinids. Walleye diet also shows major contributions from smelt, trout-perch, and centrarchids. Northern pike consumed a broader range of prey, consuming similar amounts of yellow perch and cyprinids (13% each).

Species exhibit a mean dietary trophic position estimate ranging from 3.3 to 4.4 (Fig. 1). Pumpkinseed exhibit the lowest average dietary trophic position value of 3.3, while yellow perch and rock bass average 3.7; these three species tend to be centered between what are considered (in the classical food chain sense) secondary and tertiary consumers. Smallmouth bass and largemouth bass exhibit intermediate trophic position values averaging approximately 4.0, making them tertiary consumers. The piscivores, northern pike and walleye, both exhibit trophic position estimates of 4.35 when all the available dietary data are considered, and all fish prey are assigned to trophic level 3.5. When the data are limited to include only piscivore populations for which fish prey are identified to species, the average trophic position estimate of walleye remains the same, while that of northern pike drops by 0.07 trophic level.

$\delta^{15}N$ estimates of trophic position

Average unionid mussel $\delta^{15}N$ values (reported by lake) and estimates of mean trophic position for each fish population in this study are presented in Appendix III. Seventy-eight percent of the variance in individual mussel $\delta^{15}N$ signatures is explained by the lake variable. Furthermore, the species of mussel did not vary significantly with mussel $\delta^{15}N$ (ANOVA; $p < 0.05$). Trophic position estimates were generally similar to those determined using dietary methods, with average values ranging from 3.38 in pumpkinseed to 4.40 in walleye.

The mean $\delta^{15}N$ trophic position estimates (± 1 SD) are directly compared with the mean dietary estimates of trophic position for each species (Fig. 1; Table 3). The two measures of trophic position are in close correspondence ($\delta^{15}N$ trophic position = 0.78 × dietary trophic position + 0.81; $r^2 = 0.78$). Northern pike are the only outlier, as northern pike gut content data indicate a mean trophic position value nearly 0.4 trophic level higher than the $\delta^{15}N$ trophic position estimate.

Among-population variability in trophic position

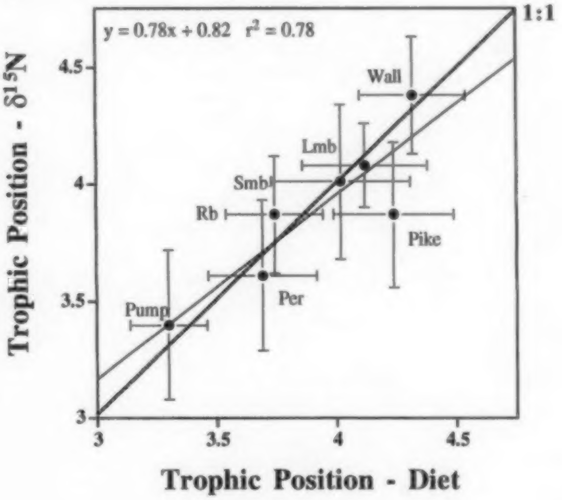
Both dietary and isotopic evidence indicates relatively high levels of among-population variability, as seen in frequency histograms of dietary and $\delta^{15}N$ trophic position values (Fig. 2). The total range of trophic position among all species spans roughly two complete trophic levels. Trophic position also varies greatly among populations of a given species. The range in trophic position for a given species is about one trophic level for each of our study species; the degree of among-population variation is similar for dietary and isotopic estimates of trophic position. The observed among-population variation in trophic

Table 2. Mean dietary data for littoral fish species included in this study.

Species	*n* lakes	*n* fish	Fish	Zoop	Ben	Pred ben	Mol	Cray	Det	Other
Pumpkinseed	27	2 000	0.0	1.6	36.2	5.6	39.9	1.3	5.5	9.7
Yellow perch	91	8 075	17.2	13.6	53.9	4.3	2.3	4.4	0.8	3.1
Rock bass	25	1 962	10.0	3.0	42.2	2.8	1.7	31.2	2.1	6.4
Smallmouth bass	79	3 162	37.6	2.0	28.8	1.2	0.1	27.3	0.7	2.3
Largemouth bass	21	5 664	53.3	4.9	11.0	9.3	0.0	10.6	1.9	8.6
Northern pike and chain pickerel	67	34 738	84.1	0.0	3.5	2.5	0.0	7.8	0.2	1.9
Walleye	32	10 386	83.3	2.0	10.7	0.5	0.0	2.5	0.2	0.8
Total	342	65 987								

Note: Zoop, zooplankton; Ben, zoobenthos; Pred ben, predatory zoobenthos; Mol, molluscs; Cray, crayfish; Det, detritus; Other, unidentified material, mammals, amphibians, birds.

Fig. 1. Comparison of mean trophic position estimates of the species included in this study, calculated using dietary and $\delta^{15}N$ methods. Error bars represent 1 SD. The bold diagonal line represents the 1:1 line.



position causes a high degree of overlap in trophic position of littoral fish species.

The distribution and variation of trophic position values calculated using the two different methods correspond quite closely. Using diet data, 1 SD in trophic position averages 0.23 trophic level (range 0.11–0.28 trophic level), while for $\delta^{15}N$ estimates, 1 SD averages 0.29 trophic level (range 0.18–0.34 trophic level).

Discussion

Role of ^{15}N in food web studies

The application of $\delta^{15}N$ as a tracer of an organism's trophic position eliminates many of the problems encountered when using diet data to estimate trophic position. Use of $\delta^{15}N$ represents the major energy flow pathways at lower trophic levels, offers a time-integrated measure of the organism's trophic position, accounts for temporal and spatial variation in feeding at multiple levels of the food web, and detects trophic interactions that are otherwise "unobservable", as gut contents can differ from the material actually assimilated by an organism.

Although use of $\delta^{15}N$ is increasingly common as a tracer of trophic relationships, the N isotopic signature of primary producers is highly variable among systems (Kling et al. 1992; Kline et al. 1993; Cabana and Rasmussen 1996) and within systems through time (Toda and Wada 1990; Gu et al. 1994; Cabana and Rasmussen 1996). As a result, $\delta^{15}N$ should reflect an organism's trophic position for single-system studies (see Hobson and Welsh 1992; Wainright et al. 1993), but the applicability of $\delta^{15}N$ as an absolute measure of trophic position (or food chain length) for comparative studies is limited because the isotopic signature of baseline organisms (phytoplankton and bacteria, which transform inorganic N into organic N) is highly variable and can be mistakenly interpreted as variation in trophic structure (Kidd et al. 1995; Wainright et al. 1996). Cabana and Rasmussen (1996) used mussel $\delta^{15}N$ signatures to correct for variability in average baseline $\delta^{15}N$ signatures. These relatively large, long-lived primary consumer organisms filter-feed on phytoplankton and bacteria in the water column (Silverman et al. 1995) and thereby serve as integrators of temporal variation in the baseline N isotopic signature. Measurement of an organism's $\delta^{15}N$ relative to that of a unionid allows a continuous measure of the organism's trophic position suitable for among-system comparisons.

Using simple and uniform assumptions, we test the $\delta^{15}N$ method by comparing the average trophic position of eight common species of fish estimated from N isotope data with estimates obtained from a large fish dietary database. The close correspondence between the estimates of trophic position based on $\delta^{15}N$ and those based on dietary data supports the validity of the isotope approach to the study of food chains proposed by Cabana and Rasmussen (1996). Although diet and $\delta^{15}N$ give corresponding estimates of average trophic position, the many advantages of $\delta^{15}N$ analysis (see above) make it a preferable measure of trophic position or food chain length for aquatic consumers. Understanding of trophic relationships is enhanced through complementary use of baseline-corrected $\delta^{15}N$ and gut content evidence. $\delta^{15}N$ is used to quantify an organism's trophic position, while diet data, although subject to error when calculating trophic position for individual communities, reveal specifically which taxa are involved in feeding interactions.

Concept of trophic position

The prevalence of omnivory and the complexity of natural food webs suggest than neither discrete food chain nor connectance food web approaches will adequately represent the pathways

Table 3. Mean trophic position for each species of fish, 1 SD of the mean trophic position, range of trophic position values, and number of fish populations, calculated using dietary and $\delta^{15}N$ methods.

	Dietary				$\delta^{15}N$			
Species	Mean trophic position	SD	Range	*n* lakes	Mean trophic position	SD	Range	*n* lakes
Pumpkinseed	3.30	0.16	3.0–3.52	27	3.38	0.33	2.81–4.15	19
Yellow perch	3.69	0.23	3.45–4.47	91	3.61	0.33	2.99–4.33	28
Rock bass	3.74	0.20	3.45–4.08	25	3.87	0.27	3.45–4.43	14
Smallmouth bass	4.02	0.29	3.46–4.50	79	4.02	0.34	3.55–4.73	15
Largemouth bass	4.12	0.26	3.55–4.49	21	4.08	0.18	3.87–4.41	7
Northern pike	4.31 (4.24)[a]	0.22	4.15–4.51	67	3.87	0.32	3.38–4.51	20
Walleye	4.33 (4.35)[a]	0.25	3.91–4.50	32	4.40	0.24	4.09–4.86	10

[a] Values in parentheses are mean trophic position estimates calculated only from populations where fish prey were identified to species.

of energy flow and mass transfer in aquatic ecosystems (Vander Zanden and Rasmussen 1996). The use of a continuous measure of trophic position attempts to strike a balance between food web approaches, which fail to weigh trophic connections according to their energetic importance, and linear food chain approaches, which ignore the omnivory and complexity that characterize ecosystems (Vander Zanden and Rasmussen 1996). Thus, trophic position quantifies, as a continuous variable, how many times the biomass consumed by an organism has been metabolically "processed" within the food chain since inorganic molecules have been first synthesized into organic compounds. Species with the same trophic position can be pooled into trophic guilds, which serve as functional groupings analogous to the trophic level, the difference being that they assume noninteger trophic position values (Vander Zanden and Rasmussen 1996). Note also that although a trophic guild includes organisms with similar trophic positions, members of a trophic guild may have different prey and different ecological niches within a food web (e.g., benthic versus pelagic predators). Use of stable C isotope ratios augments N isotope trophic position evidence by serving as a means of discriminating between benthic and pelagic sources of production (Hecky and Hesslein 1995).

Patterns in trophic position

The range in trophic position values is approximately one trophic level among populations of each of the study species. This within-species variability in trophic position can be attributed to one of two factors: highly flexible and opportunistic feeding of these fish species (Dill 1983) or variation in trophic position of prey organisms. Although this variation is likely a combination of the two sources, determining the relative importance of these sources of variation would require measurement of the trophic position of organisms situated lower in the food chain. Furthermore, our estimate of the variation accompanying mean dietary trophic position values is conservative, since it fails to account for the unknown variation in the trophic position of prey items.

Previous evidence (Rasmussen et al. 1990; Cabana and Rasmussen 1994; Vander Zanden and Rasmussen 1996) has shown that the presence/absence of pelagic forage fish and *Mysis relicta* are determinants of the trophic position of lake trout. However, the complexity of littoral food webs and the lack of presence/absence data for potential prey items make it impossible to follow a similar approach in the exploration of littoral aquatic food webs. The variability and unpredictability in trophic position among populations as shown by the $\delta^{15}N$ data presented here indicate that knowledge of the trophic position of a given population does not necessarily represent that of other populations of the same species. This is clearly shown by our trophic position data calculated from $\delta^{15}N$ where species can switch their trophic position from lake to lake (Appendix III). For example, smallmouth bass occupies a higher trophic position (4.43) than northern pike (3.69) by about 0.75 trophic level in Lake Mazinaw, but the respective trophic positions of these two species are essentially reversed in Lake Doré (trophic positions of 3.91 and 4.41 for smallmouth bass and northern pike, respectively). The impact of the presence of a particular predator on a lake community will therefore vary from lake to lake. As a result, relying on simple assumptions stereotyping the feeding ecology of a predator species will undermine our ability to predict its impact on a particular food web.

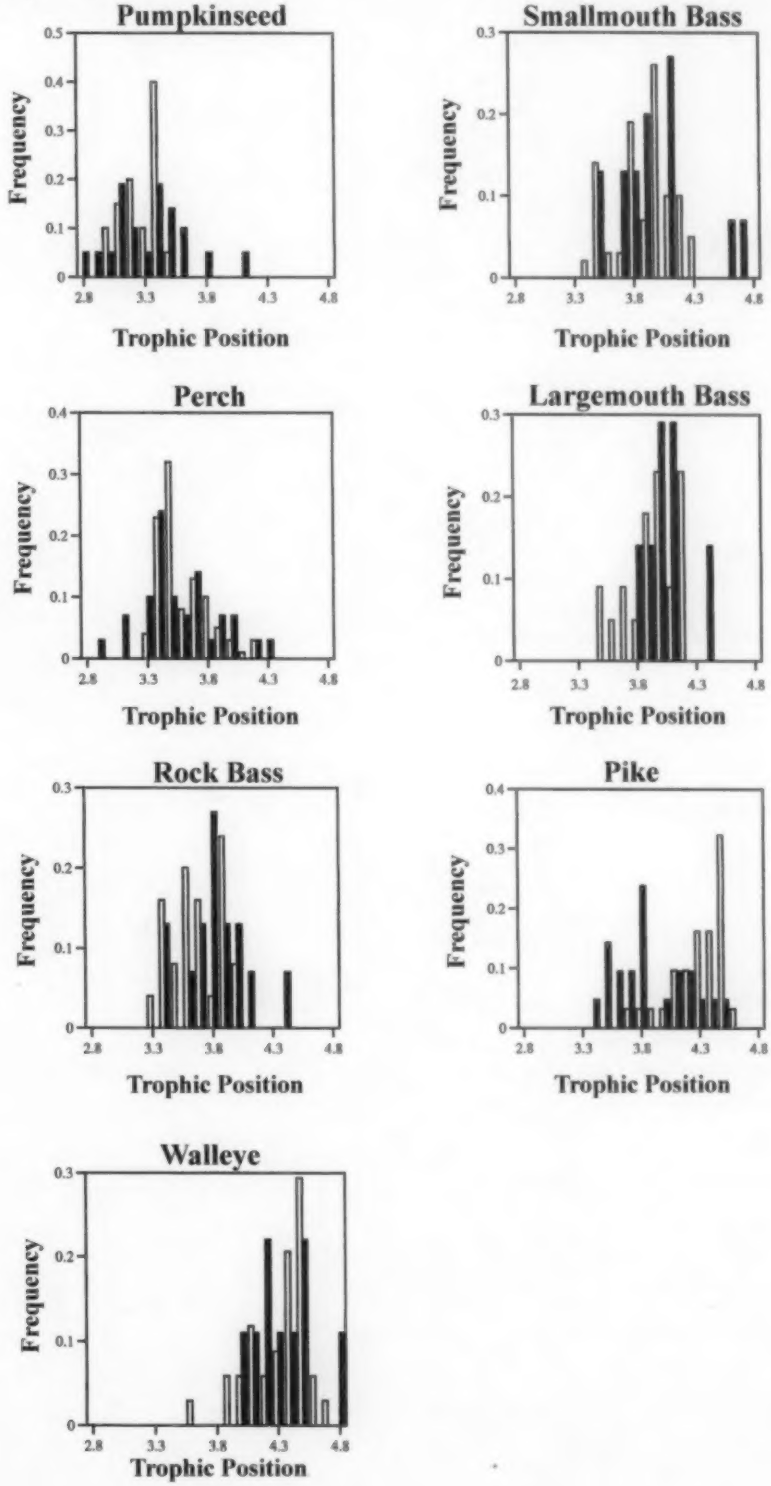
Dietary versus isotopic approaches

Although we report a close correspondence between dietary and $\delta^{15}N$ estimates of trophic position, certain limitations of the dietary approach need to be considered. One limitation is that dietary trophic position estimates require assumptions of the trophic position of prey items, thereby introducing a source of error in fish trophic position. Our estimate of 2.5 as the trophic position of zooplankton prey contrasts with Sprules and Bowerman (1988) who reported that North American zooplankton food webs have a modal food chain length varying from one to eight trophic levels (averaging between three and five trophic levels). Sprules and Bowerman (1988) tabulated food chain length without integrating omnivory into the food chain length estimate; inclusion of omnivory would result in shorter food chain length values, perhaps resembling values reported in this study.

Although our mean prey trophic position assumptions appear to be reasonable (since dietary and isotopic trophic position estimates correspond), trophic interactions among organisms at lower trophic levels remain unquantified, and may be characterized by high levels of variation. So although these assumptions appear adequate for broad-scale comparisons, as presented herein, dietary estimates of trophic position may be inadequate where detailed information for individual communities is required.

Another problem with direct comparison of dietary and $\delta^{15}N$ estimates of trophic position involves the differences in the way the two methods integrate variation in trophic position.

Fig. 2. Proportional frequency distributions of lake-specific trophic position values for littoral fish, calculated using dietary data (open bars) and baseline-corrected $\delta^{15}N$ (solid bars).



$\delta^{15}N$ provides a relatively long-term and time-integrated measure of an organism's trophic position that also accounts for variation in feeding at lower trophic levels, in addition to the higher trophic levels. Use of dietary data provides a snapshot in time of an organism's diet, which certainly does not represent the average trophic position of a population over the year. Furthermore, when calculating trophic position using dietary data, the variability accompanying the trophic position of prey items, which would be compounded up the food chain, is not passed on to predators.

Comparison of gut content and ^{15}N estimates of trophic position on a lake-specific basis can only provide a robust test of $\delta^{15}N$ where a reliable dietary estimate of trophic position is available. But an accurate measure of trophic position for an individual population requires detailed gut content data for large numbers of fish, sampled throughout the year, a situation that is rare in dietary studies. We have overcome this problem by considering the mean trophic position of large numbers of populations, which serves to reduce the error that accompanies dietary trophic position estimates for any particular lake.

Explaining the difference between $\delta^{15}N$ and dietary data for northern pike

Although $\delta^{15}N$ and dietary estimates of trophic position are in general agreement, dietary estimates for northern pike overestimate trophic position relative to $\delta^{15}N$. Determining specifically which fish taxa serve as prey of northern pike and walleye reveals the importance of yellow perch in the diet of walleye (29%) relative to northern pike (13%), while northern pike and walleye consume similar amounts of cyprinids. The high mean trophic position of yellow perch (3.7) relative to cyprinids (M.J. Vander Zanden, unpublished isotope data; DeVries and Stein 1992) may partially explain the discrepancy between $\delta^{15}N$ and dietary trophic position of northern pike.

But for studies that identify fish prey items to species, northern pike trophic position averages 4.24, compared with 4.31 when fish prey could not be further subdivided (Appendix II). The value 4.24 is in closer agreement with the $\delta^{15}N$ estimate of trophic position (3.87), although there still remains a 0.37 trophic level discrepancy between these two northern pike trophic position estimates. Breakdown of the fish prey category did not affect walleye dietary trophic position estimates (4.33 versus 4.35); gut content and $\delta^{15}N$ measures of trophic position remain in close agreement ($\delta^{15}N = 4.40$; diet = 4.35).

Although northern pike are reported to be benthic invertebrate feeders in many lakes (Chapman et al. 1989; Craig and Babaluk 1989; Chapman and Mackay 1990), these lakes were not included in this analysis because published data were presented as percent occurrence, which may not be reliably converted into a volumetric format. An effect of lake size is another possible explanation for the northern pike discrepancy. For our northern pike diet data set, lake size was positively correlated with northern pike trophic position (northern pike trophic position = 0.026(log lake area) + 4.21; $n = 36$, $p = 0.008$, $r^2 = 0.19$), and our northern pike diet study lakes tended to be larger than our $\delta^{15}N$ study lakes. Although the difference in trophic position of northern pike remains unresolved, lake-specific diet data – $\delta^{15}N$ comparisons could serve to resolve the discrepancies between the two measures of trophic position.

The presence of the additional trophic level for piscivorous fish species greatly complicates gut content trophic position estimates and introduces an additional source of error, since the trophic position of prey fish species must also be estimated. Although this was not a major problem in the simple and relatively linear pelagic systems leading to lake trout (Vander Zanden and Rasmussen 1996), estimating prey fish trophic position in the highly complex and species-rich littoral food webs becomes problematic. Although our designated trophic position estimates of littoral prey fish appear to approximate the average values for these items, our dietary calculations neglect the variation in prey trophic position, thereby underestimating the true degree of variation in average predator trophic position.

In summary, the stable isotope approach to measuring trophic structure has become widely used in ecology, offering the possibility of obtaining objective and repeatable measures of trophic position, food chain length, and omnivory (Kling et al. 1992; Hobson and Welsh 1992; Cabana and Rasmussen 1994). However, our ability to compare systems has been hampered by the problem of spatial and temporal variation in the $\delta^{15}N$ signatures at the base of the food web. Cabana and Rasmussen (1996) proposed the use of long-lived sedentary primary consumers such as unionid mussels to control for such baseline variation in $\delta^{15}N$ when calculating trophic position of consumers. The present study confirms the validity of this method by showing that $\delta^{15}N$-based estimates of trophic position in eight species of fish are strongly correlated with their trophic position estimated from dietary data.

Acknowledgments

Thanks to Jennifer Viau for laboratory assistance and Shapna Mazumder for operation of the mass spectrometer. This study was supported by a NSERC strategic grant to J.B.R. G.C. was supported by a Vineberg Fellowship. M.J.V.Z. was supported by funding from the Ontario Ministry of Natural Resources.

References

Adams, C.C., and Hankinson, T.L. 1928. The ecology and economics of Oneida lake fish. Roosevelt Wildl. Ann. **1**: 241–358.

Bennett, G.W. 1948. The bass–bluegill combination in a small artificial lake. Bull. Ill. Nat. Hist. Surv. **24**: 377–412.

Boisclair, D. 1988. Among population variability in fish growth rates: the influence of food consumption, prey type, and fish community. Ph.D. thesis, McGill University, Montreal, Que.

Bryan, S.D., Hill, T.D., Lynott, S.T., and Duffy, W.G. 1995. The influence of changing water levels and temperatures on the food habits of walleye in Lake Oahe, South Dakota. J. Freshwater Ecol. **10**: 1–10.

Bryant, H.E., and Moen, T.E. 1980. Food of largemouth bass (*Micropterus salmoides*) in Degray Reservoir, Arkansas, 1976. Ark. Acad. Sci. Proc. **34**: 34–37.

Cabana, G., and Rasmussen, J.B. 1994. Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. Nature (Lond.), **372**: 255–257.

Cabana, G., and Rasmussen, J.B. 1996. Comparing aquatic food chains using nitrogen isotopes. Proc. Natl. Acad. Sci. U.S.A. **93**: 10 844 – 10 847.

Cabana, G., Tremblay, A., Kalff, J., and Rasmussen, J.B. 1994. Pelagic food chain structure in Ontario lakes: a determinant of mercury levels in lake trout. Can. J. Fish. Aquat. Sci. **51**: 381–389.

Carpenter, S.R., Kitchell, J.F., and Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. BioScience, **35**: 381–389.

Chapman, L.J., and Mackay, W.C. 1990. Ecological correlates of feeding flexibility in northern pike (*Esox lucius*). J. Freshwater Ecol. **5**: 313–322.

Chapman, L.J., Mackay, W.C., and Wilkinson, C.W. 1989. Feeding flexibility in northern pike (*Exox lucius*): fish versus invertebrate prey. Can. J. Fish. Aquat. Sci. **46**: 666–669.

Clady, M.D. 1974. Food habits of yellow perch, smallmouth bass and largemouth bass in two unproductive lakes in Northern Michigan. Am. Midl. Nat. **91**: 453–459.

Clemens, W.A., Dymond, J.R., Bigelow, N.K., Adamstone, F.B., and Harkness, W.J.K. 1923. The food of Lake Nipigon fishes. Univ. Toronto Stud. Biol. **22**: 173–188.

Clemens, W.A., Dymond, J.R., and Bigelow, N.K. 1924. Food studies of Lake Nipigon fishes. Univ. Toronto Stud. Biol. **25**: 103–165.

Cooper, G.P. 1941. A biological survey of lakes and ponds of the Androscoggin and Kennebec River Drainage Systems in Maine. Maine Dep. Inland Fish. Game Fish Surv. Rep. No. 4.

Cooper, G.P. 1942. A biological survey of lakes and ponds of the central coastal area of Maine. Maine Dep. Inland Fish. Game Fish Surv. Rep. No. 5.

Couey, F.M. 1935. Fish food studies of a number of northeastern Wisconsin lakes. Wis. Acad. Sci. Art. Lett. **29**: 131–172.

Craig, J.F., and Babaluk, J.A. 1989. Relationship of condition of walleye (*Stizostedion vitreum*) and northern pike (*Esox lucius*) to water clarity, with special reference to Dauphin Lake, Manitoba. Can. J. Fish. Aquat. Sci. **46**: 1581–1586.

Cummins, K.W., and Wuycheck, J.C. 1971. Caloric equivalents for investigations in ecological energetics. Int. Assoc. Theor. Appl. Limnol. **18**: 1–158.

DeVries, D.R., and Stein, P.A. 1992. Complex interactions between fish and zooplankton: quantifying the role of an open-water planktivore. Can. J. Fish. Aquat. Sci. **49**: 1216–1227.

Diana, J.S. 1979. The feeding pattern and daily ration of a top carnivore, the northern pike (*Esox lucius*). Can. J. Zool. **57**: 2121–2127.

Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. Can. J. Fish. Aquat. Sci. **40**: 398–408.

Doan, K.H. 1940. Studies of the smallmouth bass. J. Wildl. Manage. **4**: 241–267.

Driver, E.A., Sugden, L.G., and Kovach, R.J. 1974. Calorific, chemical and physical values of potential duck foods. Freshwater Biol. **4**: 281–292.

Etnier, D.A. 1971. Food of three species of sunfishes (*Lepomis, Centrarchidae*) and their hybrids in three Minnesota lakes. Trans. Am. Fish. Soc. **100**: 124–128.

Fedoruk, A.N. 1966. Feeding relationships of walleye and smallmouth bass. J. Fish. Res. Board Can. **22**: 941–943.

Flemer, D.A., and Woolcott, W.S. 1966. Food habits and distribution of the fishes of Tuckahoe Creek, Virginia, with special emphasis on the bluegill, *Lepomis m. macrochirus* Rafinesque. Chesapeake Sci. **7**: 75–89.

Foote, L.E., and Blake, B.P. 1945. Life history of the eastern pickerel in Babcock Pond, Connecticut. J. Wildl. Manage. **9**: 89–96.

Fox, M.G., and Keast, A. 1990. Effects of winterkill on population structure, body size, and prey consumption patterns of pumpkinseed in isolated beaver ponds. Can. J. Zool. **68**: 2489–2498.

Fraser, J.M. 1978. The effect of competition with yellow perch on the survival and growth of planted brook trout, splake, and rainbow trout in a small Ontario lake. Trans. Am. Fish. Soc. **107**: 505–517.

Griswold, B.L., and Tubb, R.A. 1977. Food of yellow perch, white bass, freshwater drum, and channel catfish in Sandusky Bay, Lake Erie. Ohio J. Sci. **77**: 43–47.

Gu, B., Schell, D.M., and Alexander, V. 1994. Stable carbon and nitrogen isotopic analysis of the plankton food web in a subarctic lake. Can. J. Fish. Aquat. Sci. **51**: 1338–1344.

Hazel, P.P., and Fortin, R. 1986. Le doré jaune (*Stizostedion vitreum* Mitchill) au Québec: biologie et gestation. Ministère du Loisir, de la Chasse et de la Pêche, Québec, Qué.

Hecky, R.E., and Hesslein, R.H. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. J. N. Am. Benthol. Soc. **14**: 631–653.

Herman, M.L., Campbell, R.S., and Redmond, L.C. 1969. Manipulation of fish populations through reservoir drawdown. Trans. Am. Fish. Soc. **98**: 293–304.

Hesslein, R.H., Hallard, K.A., and Ramlal, P. 1993. Replacement of sulfur, carbon, and nitrogen in tussue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by ^{34}S, ^{13}C, and ^{15}N. Can. J. Fish. Aquat. Sci. **50**: 2071–2076.

Hobson, K.A., and Welsh, H.E. 1992. Determination of trophic relationships within a high Arctic marine food web using δ^{13}C an δ^{15}N analysis. Mar. Ecol. Prog. Ser. **84**: 9–18.

Hodgson, J.R., Carpenter, S.R., and Gripentrog, A.P. 1989. Effect of sampling frequency on intersample variance and food consumption estimates of nonpiscivorous largemouth bass. Trans. Am. Fish. Soc. **118**: 11–19.

Hodgson, J.R., Hodgson, C.J., and Brooks, S.M. 1991. Trophic interaction and competition between largemouth bass (*Micropterus salmoides*) and rainbow trout (*Oncorhynchus mykiss*) in a manipulated lake. Can. J. Fish. Aquat. Sci. **48**: 1704–1712.

Hunt, B.P., and Carbin, W.F. 1950. Food of young pike, *Esox lucius*, and associated fishes in Peterson's ditches, Houghton Lake, Michigan. Trans. Am. Fish. Soc. **79**: 67–83.

Hunt, R.L. 1965. Food of northern pike in a Wisconsin trout stream. Trans. Am. Fish. Soc. **94**: 95–97.

Hunter, G.W. III, and Rankin, J.S. Jr. 1939. The food of pickerel. Copeia, **4**: 194–199.

Hurley, D.A., and Christie, W.J. 1977. Depreciation of the warmwater fish community in the Bay of Quinte, Lake Ontario. J. Fish. Res. Board Can. **34**: 1849–1860.

Johnson, F.H. 1977. Response of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations to removal of white sucker (*Catastomus commersoni*) from a Minnesota lake, 1966. J. Fish. Res. Board Can. **34**: 1633–1642.

Johnson, F.H., and Hale, J.G. 1977. Interrelations between walleye (*Stizostedion vitreum vitreum*) and smallmouth bass (*Micropterus dolomieui*) in four northeastern Minnesota lakes, 1948–69. J. Fish. Res. Board Can. **34**: 1626–1632.

Johnson, J.H., and Dropkin, D.S. 1995. Diel feeding chronology of six fish species in the Juniata River, Pennsylvania. J. Freshwater Ecol. **10**: 11–18.

Johnson, L. 1972. Keller Lake: characteristics of a culturally unstressed salmonid community. J. Fish. Res. Board Can. **29**: 731–740.

Keast, A. 1977. Diet overlaps and feeding relationships between the year classes in the yellow perch (*Perca flavescens*). Environ. Biol. Fishes, **2**: 53–70.

Keast, A., and Welsh, L. 1968. Daily feeding periodicities, food uptake rates, and dietary changes with h of day in some lake fishes. J. Fish. Res. Board Can. **25**: 1133–1144.

Kelso, J.R. 1973. Seasonal energy changes in walleye and their diet in West Blue Lake, Manitoba. Trans. Am. Fish. Soc. **103**: 363–368.

Kelso, J.R.M., and Ward, F.J. 1977. Unexploited percid populations of West Blue Lake, Manitoba, and their interactions. J. Fish. Res. Board Can. **34**: 1655–1669.

Kerr, S.R., and Martin, N.V. 1970. Tropho-dynamics of lake trout production systems. *In* Marine food chains. *Edited by* J.H. Steele. Oliver and Boyd, Edinburgh, U.K. pp. 365–376.

Kidd, K.A., Schindler, D.W., Hesslein, R.H., and Muir, D.C.G. 1995. Correlations between stable nitrogen isotope ratios and concentrations of organochlorines in biota from a freshwater food web. Sci. Total Environ. **161**: 381–390.

Kline, T.C., Goering, J.J., Mathisen, O.A., Poe, P.H., Parker, P.L., and Scalan, R.S. 1993. Recycling of elements transported upstream by runs of Pacific salmon: II. δ^{15}N and δ^{13}C evidence in the Kvichak River watershed, Bristol Bay, Southwestern Alaska. Can. J. Fish. Aquat. Sci. **50**: 2350–2365.

Kling, G.W., Fry, B., and O'Brien, W.J. 1992. Stable isotopes and planktonic trophic structure in arctic lakes. Ecology, **73**: 561–566.

Knight, R.L., Margraf, F.J., and Carline, R.F. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. Trans. Am. Fish. Soc. **113**: 677–693.

Lagler, K.F. 1956. The pike, *Esox lucius* Linnaeus, in relation to waterfowl on the Seney National Wildlife Refuge, Michigan. J. Wildl. Manage. **20**: 114–124.

Laughlin, D.R., and Werner, E.E. 1980. Resource partitioning in two coexisting sunfish: pumpkinseed (*Lepomis gibbosus*) and northern longear sunfish (*Lepomis megalotis peltastes*). Can. J. Fish. Aquat. Sci. **37**: 1411–1420.

Lawler, G.H. 1965. The food of the pike, *Esox lucius*, in Heming lake, Manitoba. J. Fish. Res. Board Can. **22**: 1357–1377.

Lawrence, S.G., Malley, D.F., Findlay, W.J., MacIver, M.A., and Delbaere, I.L. 1987. Method for estimating dry weight of freshwater planktonic crustaceans from measures of length and shape. Can. J. Fish. Aquat. Sci. **44**: 264–274.

Levine, S. 1980. Several measures of trophic structure applicable to complex food webs. J. Theor. Biol. **83**: 195–207.

Lindeman, R.L. 1942. The tropho-dynamic aspect of ecology. Ecology, **23**: 399–418.

Lyons, J., and Magnuson, J.J. 1987. Effects of walleye predation on the population dynamics of small littoral zone fishes in a northern Wisconsin lake. Trans. Am. Fish. Soc. **116**: 29–39.

Mathers, R.A., and Johansen, P.H. 1985. The effects of feeding ecology on mercury accumulation in walleye (*Stizostedion vitreum*) and pike (*Esox lucius*) in Lake Simcoe. Can. J. Zool. **63**: 2006–2012.

McIlwain, T.D. 1970. Stomach contents and length–weight relationships of chain pickerel (*Esox niger*) in south Mississippi waters. Trans. Am. Fish. Soc. **99**: 439–440.

Miller, S.J., and Storck, T. 1984. Temporal spawning distribution of largemouth bass and young-of-the-year, determined from daily otolith rings. Trans. Am. Fish. Soc. **113**: 571–578.

Mills, E.L., and Forney, J.L. 1981. Energetics, food consumption, and growth of young yellow perch in Oneida Lake, New York. Trans. Am. Fish. Soc. **110**: 479–488.

Minagawa, M., and Wada, E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. Geochim. Cosmochim. Acta, **48**: 1135–1140.

Moffett, J.W., and Hunt, B.P. 1943. Winter feeding habits of bluegill, *Lepomis macrochirus* (Rafinesque), and yellow perch, *Perca flavescens* (Mitchill), in Cedar Lake, Washtenaw County, Michigan. Trans. Am. Fish. Soc. **73**: 231–242.

Murdoch, W.W. 1966. Community structure, population control, and competition — a critique. Am. Nat. **100**: 219–226.

Nakashima, B.S., and Leggett, W.C. 1975. Yellow perch (*Perca flavescens*) biomass responses to different levels of phytoplankton and benthic biomass in Lake Memphremagog, Quebec–Vermont. J. Fish. Res. Board Can. **32**: 1785–1797.

Owens, N.J.P. 1987. Natural variation in ^{15}N in the marine environment. Adv. Mar. Biol. **24**: 390–451.

Paine, R.T. 1988. Food webs: road maps of interaction or grist for theoretical development? Ecology, **69**: 1648–1654.

Parks, C.E. 1949. The summer food of some game fishes of Winona Lake. Invest. Ind. Lakes Streams, **3**: 235–245.

Parrish, D.L., and Margraf, F.J. 1990. Interactions between white perch (*Morone americana*) and yellow perch (*Perca flavescens*) in Lake Erie as determined from feeding and growth. Can. J. Fish. Aquat. Sci. **47**: 1779–1787.

Parrish, D.L., and Margraf, F.J. 1994. Spatial and temporal patterns of food use by white perch and yellow perch in Lake Erie. J. Freshwater Ecol. **9**: 29–35.

Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. **18**: 293–320.

Polis, G.A. 1991. Complex trophic interactions in deserts: an empirical critique of food web theory. Am. Nat. **138**: 123–155.

Priegel, G.R. 1963. Food of walleye and sauger in Lake Winnebago, Wisconsin. Trans. Am. Fish. Soc. **92**: 312–313.

Probst, W.E., Rabeni, C.F., Covington, W.G., and Marteney, R.E. 1984. Resource use by stream-dwelling rock bass and smallmouth bass. Trans. Am. Fish. Soc. **113**: 283–294.

Raney, E.C. 1942. The summer food and habits of the chain pickerel (*Esox niger*) of a small New York pond. J. Wildl. Manage. **6**: 58–66.

Rasmussen, J.B., Rowan, D.J., Lean, D.R.S., and Carey, J.H. 1990. Food chain structure in Ontario lakes determines PCB levels in lake trout (*Salvelinus namaycush*) and other pelagic fish. Can. J. Fish. Aquat. Sci. **47**: 2030–2038.

Rawson, D.S. 1930. The bottom fauna of Lake Simcoe and its role in the ecology of the lake. Univ. Toronto Stud. Biol. **40**: 1–123.

Rawson, D.S. 1951. Studies of the fish of Great Slave Lake. J. Fish. Res. Board Can. **8**: 207–240.

Rawson, D.S. 1959. Limnology and fisheries of Cree and Wollaston lakes in northern Saskatchewan. Fish. Branch Dep. Nat. Resour. Sask. Fish. Rep. **4**: 5–73.

Rawson, D.S. 1965. The life history and ecology of the yellow walleye, *Stizostedion vitreum*, in Lac La Ronge, Saskatchewan. Trans. Am. Fish. Soc. **86**: 15–37.

Sadzikowski, M.R., and Wallace, D.C. 1976. A comparison of the food habits of size classes of three sunfishes (*Lepomis macrochirus* Rafinesque, *L. gibbosus* Linnaeus and *L. cyanellus* Rafinesque). Am. Midl. Nat. **95**: 220–225.

Saiki, M.K., and Tash, J.C. 1978. Unusual population dynamics in largemouth bass, *Micropterus salmoides* (Lacepede), caused by a seasonally fluctuating food supply. Am. Midl. Nat. **100**: 116–125.

Schaeffer, J.S., and Margraf, F.J. 1986. Food of white perch (*Morone americana*) and potential for competition with yellow perch (*Perca flavescens*) in Lake Erie. Ohio J. Sci. **86**: 26–29.

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. No. 184.

Seaburg, K.G., and Moyle, J.B. 1964. Feeding habits, digestive rates, and growth of some Minnesota warmwater fishes. Trans. Am. Fish. Soc. **93**: 269–285.

Serns, S.L., and Hoff, M.H. 1984. Food habits of adult yellow perch and smallmouth bass in Nebish lake, Wisconsin — with special reference to zooplankton density and composition. Tech. Bull. No. 149. Department of Natural Resources. Madison, Wis.

Silverman, H., Achberger, E.C., Lynn, J.W., and Dietz, T.H. 1995. Filtration and utilization of laboratory-cultured bacteria by *Dressena polymorpha*, *Corbicula fluminea*, and *Carunculina texasensi*. Biol. Bull. Mar. Biol. Woods Hole, **187**: 308–319.

Smock, L.A. 1980. Relationship between body size and biomass of aquatic insects. Freshwater Biol. **10**: 375–383.

Snetsinger, M.A. 1992. Resource division in a pond impoundment fish community with comparisons to other small water body systems. M.Sc. thesis, Queens University, Kingston, Ont.

Snow, H.E. 1971. Harvest and feeding habits of largemouth bass in Murphy Flowage, Wisconsin. Tech. Bull. No. 50. Department of Natural Resources, Madison, Wis.

Sprules, W.G., and Bowerman, J.E. 1988. Omnivory and food chain length in zooplankton food webs. Ecology, **69**: 418–425.

Storck, T.W. 1986. Importance of gizzard shad in the diet of largemouth bass in Lake Shelbyville, Illinois. Trans. Am. Fish. Soc. **115**: 21–27.

Surber, E.W. 1941. A quantitative study of the food of the smallmouth black bass, *Micropterus dolomieu*, in three eastern streams. Trans. Am. Fish. Soc. **70**: 311–324.

Swenson, W.A., and Smith, L.L. Jr. 1976. Influence of food competition, predation, and cannibalism on walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) populations in Lake of the Woods, Minnesota. J. Fish. Res. Board Can. **33**: 1946–1954.

Tester, A.L. 1932. Food of the small-mouthed black bass (*Micropterus dolomieu*) in some Ontario waters. Univ. Toronto Stud. Biol. **22**: 171–203.

Tharratt, R.C. 1959. Food of the yellow perch, *Perca flavescens* (Mitchill) in Saginaw Bay, Lake Huron. Trans. Am. Fish. Soc. **88**: 330–331.

Toda, H., and Wada, E. 1990. Use of $^{15}N/^{14}N$ ratios to evaluate the food source of the mysid, *Neomysis intermedia* Czerniawsky, in a eutrophic lake in Japan. Hydrobiologia, **194**: 85–90.

Vadas, R.L. Jr. 1990. The importance of omnivory and predator regulation of prey in freshwater fish assemblages of North America. Environ. Biol. Fishes, **27**: 285–302.

Vallieres, L., and Fortin, R. 1988. Le grand brochet (*Esox lucius*) au Québec: biologie et gestation. Ministère du Loisir, de la chasse et de la Pêche, Québec, Qué.

Vander Zanden, M.J., and Rasmussen, J.B. 1996. A trophic position model of pelagic food webs: impact on contaminant biomagnification in lake trout. Ecol. Monogr. **66**: 451–477.

Wagner, W.C. 1972. Utilization of alewives by inshore piscivorous fishes in Lake Michigan. Trans. Am. Fish. Soc. **101**: 55–63.

Wainright, S.C., Fogarty, M.J., Greenfield, R.C., and Fry, B. 1993. Long-term changes in the Georges Bank food web: trends in stable isotope compositions of fish scales. Mar. Biol. **115**: 481–493.

Wainright, S.C., Fuller, C.M., Michener, R.H., and Richards, R.A. 1996. Spatial variation of trophic position and growth rate of juvenile striped bass (*Morone saxatilis*) in the Delaware River. Can. J. Fish. Aquat. Sci. **53**: 685–692.

Ward, F.J., and Robinson, G.G.C. 1974. A review of research on the limnology of West Blue Lake, Manitoba. J. Fish. Res. Board Can. **31**: 977–1005.

Weisberg, S.B., and Janicki, A.J. 1990. Summer feeding patterns of white perch, channel catfish, and yellow perch in the Susquehanna River, Maryland. J. Freshwater Ecol. **5**: 391–405.

Winemiller, K.O. 1990. Spatial and temporal variation in tropical fish trophic networks. Ecol. Monogr. **60**: 331–367.

Wolfert, D.R., and Miller, T.J. 1978. Age, growth, and food of northern pike in Eastern Lake Ontario. Trans. Am. Fish. Soc. **107**: 696–702.

Wooton, J.T., and Power, M.E. 1993. Productivity, consumers, and the structure of a river food chain. Proc. Natl. Acad. Sci. U.S.A. **90**: 1384–1387.

Appendix I. Study lake, location (State or Province), year, sample size, dietary data, trophic position, and data source.

Lake	Location	Year	*n* fish	Prey category								Trophic position	Reference[a]
				Fish	Zoop	Ben	Pred ben	Mol	Cray	Det	Other		
				Pumpkinseed (total *n* = 2000 fish)									
10 lakes	Maine	1938	101	0.0	0.2	17.4	0.0	61.5	0.0	20.9	0.0	3.09	1
Bassen	Michigan	1977	50	0.0	0.0	34.5	16.1	28.8	0.0	0.0	21.0	3.44	3
Deep	Michigan	1977	50	0.0	0.0	29.9	0.0	17.4	0.0	0.0	53.0	3.42	3
Dowsley Pond	Ontario	1987	280	0.0	0.0	62.8	15.3	16.7	0.0	0.0	5.0	3.49	4
Hamilton	Michigan	1977	50	0.0	0.0	1.8	0.1	58.9	0.0	0.0	39.0	3.20	3
Little Cataraqui Cr.	Ontario	1990	187	0.0	12.8	62.2	6.2	14.1	0.0	1.9	2.9	3.45	5
Long	Minnesota	1962	8	0.0	0.0	17.8	4.4	77.7	0.0	0.0	0.0	3.13	6
Maple	Minnesota	1957	367	0.0	0.0	39.0	0.0	49.0	0.0	3.5	9.5	3.25	7
Opinicon	Ontario	1987	280	0.0	4.7	13.3	5.3	71.3	0.0	0.0	5.3	3.17	4
Opinicon	Ontario	1966	103	0.0	3.7	57.7	21.3	12.3	2.3	0.0	0.0	3.52	8
Shaw	Michigan	1977	50	0.0	0.0	0.2	0.0	99.7	0.0	0.0	0.0	3.00	3
Sieverson	Minnesota	1962	66	0.0	0.0	16.9	3.9	79.2	0.0	0.0	0.0	3.12	6
Sister	Michigan	1972	65	0.0	3.9	40.9	4.6	28.8	0.0	5.0	16.7	3.35	9
Squaw	Minnesota	1962	25	0.0	0.0	42.6	3.0	33.5	20.3	0.0	0.6	3.45	6
Tuckahoe Creek	Virginia	1958	35	0.0	0.2	79.1	0.0	0.0	0.0	20.7	0.0	3.40	10
U. Poole Pond	Ontario	1987	280	0.0	2.0	46.3	14.3	29.3	0.0	0.0	8.0	3.43	4
Winona	Wisconsin	1940	3	0.0	0.0	52.3	0.0	0.0	0.0	41.6	4.0	3.26	11
Mean				0.0	1.6	36.2	5.6	39.9	1.3	5.5	9.7	3.30	
				Yellow perch (total *n* = 8075 fish)									
10 lakes	Maine	1938	30	71.6	1.2	15.7	0.8	0.0	0.0	10.7	0.0	4.17	1
7 lakes	Maine	1941	78	78.3	0.3	6.2	14.8	0.3	0.0	0.1	0.0	4.36	1
Alle	Wisconsin	1931	3	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	3.50	12
Arbor	Wisconsin	1931	8	0.0	0.0	89.5	0.0	0.0	0.0	0.0	9.0	3.48	12
Brome	Quebec	1984	17	0.0	0.0	97.0	0.0	3.0	0.0	0.0	0.0	3.48	13
Bromont	Quebec	1984	34	14.3	2.6	53.0	25.8	0.0	0.0	0.0	4.2	3.77	13
Brompton	Quebec	1984	34	26.5	0.0	69.7	0.3	3.5	0.0	0.0	0.0	3.75	13
Cedar	Michigan	1941	112	80.7	12.0	7.3	0.0	0.0	0.0	0.0	0.0	4.31	14
Clear	Wisconsin	1931	13	11.0	0.0	86.5	0.0	0.0	0.0	1.5	0.0	3.59	12
Clear	Wisconsin	1932	7	6.0	6.0	80.0	0.0	3.0	5.0	0.0	0.0	3.57	12
Crane	Wisconsin	1932	11	10.5	0.0	85.5	0.0	0.0	0.0	0.0	4.0	3.61	12
Crystal	Wisconsin	1931	9	56.5	2.0	33.0	0.0	0.0	0.0	0.0	8.0	4.06	12

Appendix I (*continued*).

				Prey category									
Lake	Location	Year	*n* fish	Fish	Zoop	Ben	Pred ben	Mol	Cray	Det	Other	Trophic position	Reference[a]
Cub	Michigan	1974	201	24.5	1.8	37.8	27.0	2.5	0.0	0.0	6.0	3.86	15
D'Argent	Quebec	1984	34	0.0	11.2	86.2	0.0	1.6	0.0	0.9	0.0	3.49	13
Drolet	Quebec	1984	17	0.0	19.1	76.9	3.3	0.7	0.0	0.0	0.0	3.51	13
Erie	Ohio	1971	436	21.4	14.2	48.9	0.0	0.0	0.0	0.0	15.5	3.71	16
Erie	Ohio	1983	—	4.0	37.0	59.0	0.0	0.0	0.0	0.0	0.0	3.54	17
Erie	Ohio	1984	—	14.5	53.6	31.9	0.0	0.0	0.0	0.0	0.0	3.65	17
Erie	Ohio	1985	—	7.8	34.9	57.3	0.0	0.0	0.0	0.0	0.0	3.58	17
Erie	Ohio	1983	8	3.0	28.0	59.0	0.0	10.0	0.0	0.0	0.0	3.48	18
Erie	Ohio	1984	20	16.0	58.0	23.0	0.0	3.0	0.0	0.0	0.0	3.65	18
Erie	Ohio	1985	13	5.0	43.0	48.0	0.0	4.0	0.0	0.0	0.0	3.53	18
Western Basin (Erie)	Ohio	1981	82	19.6	53.9	23.4	0.0	3.2	0.0	0.0	0.0	3.68	19
Geneva	Wisconsin	1921	19	5.3	40.0	40.0	0.0	0.0	0.0	0.0	15.0	3.56	20
Hertel	Quebec	1984	17	0.0	13.5	80.8	0.0	5.7	0.0	0.0	0.0	3.47	13
Houghton	Michigan	1939	78	24.6	6.0	69.4	0.0	0.0	0.0	0.0	0.0	3.75	21
Houghton	Michigan	1940	267	69.1	1.8	27.8	1.3	0.0	0.0	0.0	0.7	4.21	21
Saginaw Bay (Huron)	Ontario	1956	241	12.0	23.0	48.0	0.0	6.0	0.0	0.0	11.0	3.59	22
Little Minnow	Ontario	1970–75	312	10.0	5.0	22.0	40.0	0.0	8.0	0.0	15.0	3.84	23
Long	Wisconsin	1931	98	5.0	43.5	37.5	0.0	0.0	0.0	0.0	15.0	3.57	12
Magog	Quebec	1984	17	0.0	0.6	83.8	0.0	8.2	7.4	0.0	0.0	3.50	13
Maple	Minnesota	1957	97	49.0	0.0	40.0	0.0	1.5	0.0	0.0	10.0	3.99	7
Massawippi	Quebec	1984	17	0.0	11.4	60.0	26.0	2.6	0.0	0.0	0.0	3.62	13
Memphramagog	Quebec	1984	34	8.0	1.7	86.1	3.4	0.8	0.0	0.0	0.0	3.59	13
Muskellunge	Wisconsin	1931	207	48.0	14.0	20.0	0.0	2.0	1.0	6.0	9.5	3.95	12
Muskellunge	Wisconsin	1932	375	17.5	15.5	39.1	0.0	5.0	0.0	1.0	21.0	3.63	12
Nebish	Wisconsin	1931	109	2.5	1.5	89.2	0.0	5.5	0.0	0.1	2.5	3.52	12
Nebish	Wisconsin	1932	178	2.5	21.5	63.6	0.0	5.0	0.0	0.0	6.0	3.48	12
Nebish	Wisconsin	1977	102	23.5	5.1	58.9	10.9	1.6	0.0	0.0	0.0	3.78	24
Nebish	Wisconsin	1978	122	7.6	4.1	77.0	6.0	0.8	0.0	4.5	0.0	3.58	24
Nebish	Wisconsin	1979	92	24.0	2.3	58.4	6.7	5.0	0.0	3.6	0.0	3.73	24
Nebish	Wisconsin	1980	123	3.0	2.1	16.0	4.2	1.8	72.0	0.9	0.0	3.90	24
Nebish	Wisconsin	1981	111	34.2	9.4	38.1	5.7	10.8	0.0	1.7	0.0	3.81	24
Nipigon	Ontario	1921	14	7.1	36.8	56.1	0.0	0.0	0.0	0.0	0.0	3.57	25
Nipigon	Ontario	1921	43	25.5	8.5	55.0	0.0	0.0	4.0	0.0	7.0	3.78	26
Nipigon	Ontario	1927	—	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	3.50	27
Oneida	New York	1975	254	0.0	91.8	8.2	0.0	0.0	0.0	0.0	0.0	3.50	28
Oneida	New York	1976	212	0.0	88.5	11.5	0.0	0.0	0.0	0.0	0.0	3.50	28
Oneida	New York	1977	232	0.0	73.7	26.3	0.0	0.0	0.0	0.0	0.0	3.50	28
Oneida	New York	1927	—	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	3.50	27
Opinicon	Ontario	1966	79	0.0	11.5	62.5	24.0	0.0	1.5	0.0	0.0	3.62	8
Opinicon	Ontario	1971	1033	18.4	11.5	13.6	30.9	2.8	19.6	0.0	3.2	3.87	29
Opinicon	Ontario	1972	49	7.5	17.0	5.0	48.0	2.0	15.0	0.0	0.0	3.80	29
Opinicon	Ontario	1973	49	9.5	19.5	8.0	33.0	1.0	14.0	0.0	0.0	3.60	29
Pallette	Wisconsin	31	8	55.0	0.0	33.0	0.0	13.5	0.0	0.0	0.0	4.01	12
Pepin	Wisconsin	1921	15	11.3	18.8	59.6	0.0	5.8	0.0	0.0	4.0	3.58	20
Plum	Wisconsin	1931	15	31.5	0.0	13.5	0.0	0.5	50.5	0.0	3.0	4.05	12
Rock	Wisconsin	1931	23	33.5	0.1	51.5	0.0	0.5	0.0	12.0	3.5	3.79	12
Roxton	Quebec	1984	34	0.0	0.0	96.9	0.0	3.1	0.0	0.0	0.0	3.48	13
Silver	Quebec	1984	17	0.0	0.1	89.3	8.4	2.0	0.0	0.0	0.0	3.53	13
Silver	Wisconsin	1931	176	6.5	9.5	57.1	0.0	3.5	11.0	2.0	8.0	3.56	12
Silver	Wisconsin	1932	273	96.0	0.0	2.0	0.0	0.0	2.0	0.0	0.0	4.47	12
Simcoe	Ontario	1927	13	11.0	0.0	77.0	0.0	4.0	8.0	0.0	0.0	3.63	27
Spider	Wisconsin	1931	32	25.0	0.0	15.5	0.0	3.0	48.5	4.0	5.0	3.97	12
Starr	Wisconsin	1931	4	0.0	0.0	68.5	0.0	0.0	31.5	0.0	0.0	3.66	12
Susquehanna R.	Maryland	1982	698	2.0	0.0	79.0	0.0	15.0	0.0	0.0	4.0	3.45	30
Trout	Wisconsin	1931	160	36.0	4.0	35.7	0.0	1.0	16.0	2.0	4.5	3.91	12
Trout	Wisconsin	1932	106	39.0	0.0	43.1	0.0	6.0	1.0	1.5	9.0	3.85	12

Appendix I (*continued*).

Lake	Location	Year	n fish	Prey category								Trophic position	Reference[a]
				Fish	Zoop	Ben	Pred ben	Mol	Cray	Det	Other		
Vieux	Wisconsin	1931	35	13.5	0.0	79.5	0.0	0.0	0.0	4.0	2.5	3.61	12
Vieux	Wisconsin	1932	76	6.0	0.1	84.0	0.0	4.5	0.0	0.5	5.0	3.54	12
Waskesiu	Saskatchewan	1927	—	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	3.50	27
Waterloo	Quebec	1984	34	0.0	1.8	91.1	5.2	1.8	0.0	0.0	0.0	3.52	13
Weber	Wisconsin	1931	178	6.5	2.5	85.6	0.0	0.1	0.0	0.5	5.0	3.57	12
Weber	Wisconsin	1932	184	1.0	14.0	80.7	0.0	0.5	0.0	0.0	2.0	3.48	12
West Blue	Manitoba	1971	240	5.5	21.8	45.5	0.0	0.0	3.8	0.0	23.0	3.57	31
Winona	Wisconsin	1940	6	40.0	0.0	33.6	0.0	10.4	16.0	0.0	0.0	3.93	11
Mean				17.2	13.6	53.9	4.3	2.3	4.4	0.8	3.1	3.69	
Rock bass (total n = 1962 fish)													
Alle	Wisconsin	1931	10	0.0	0.0	0.0	0.0	0.0	93.0	1.0	3.0	3.94	12
Bear	Wisconsin	1931	12	0.0	0.0	40.5	0.0	3.5	47.0	0.0	9.0	3.72	12
Clear	Wisconsin	1931	4	0.0	0.0	37.5	0.0	0.0	58.5	0.0	4.0	3.79	12
Clear	Wisconsin	1932	3	0.0	0.0	97.0	0.0	3.0	0.0	0.0	0.0	3.49	12
Georgian Bay (Huron)	Ontario	1928	40	28.5	0.0	10.2	0.0	0.0	60.4	0.9	0.0	4.08	32
Goose Creek	Virginia	1986	40	0.0	14.0	86.0	0.0	0.0	0.0	0.0	0.0	3.50	33
Muskellunge	Wisconsin	1931	338	12.5	0.0	41.0	0.0	3.0	13.5	11.0	6.0	3.68	12
Muskellunge	Wisconsin	1932	371	12.0	0.1	58.8	0.0	0.5	5.5	2.0	20.5	3.63	12
Nebish	Wisconsin	1931	184	3.5	7.5	81.1	0.0	5.0	0.0	0.1	2.0	3.50	12
Nebish	Wisconsin	1932	209	7.5	3.5	79.7	0.0	0.5	0.0	0.1	6.0	3.53	12
Nebish	Wisconsin	1932	27	3.5	50.5	31.5	0.0	12.0	0.0	0.0	2.0	3.47	12
Nipissing	Ontario	1929-30	12	19.1	0.0	16.1	0.0	0.0	64.6	0.2	0.0	4.01	32
Opinicon	Ontario	1966	96	10.0	0.0	6.7	52.7	0.0	30.0	0.0	0.0	4.00	8
Ozark streams	Arkansas	1980	210	9.0	0.0	18.0	0.0	0.0	73.0	0.0	0.0	3.96	34
Pallette	Wisconsin	1931	11	0.0	0.0	92.0	0.0	5.0	0.0	0.0	1.0	3.45	12
Plum	Wisconsin	1931	1	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	4.00	12
Rock	Wisconsin	1931	4	24.5	0.0	61.5	0.0	0.0	0.0	4.0	10.0	3.73	12
Silver	Wisconsin	1931	124	5.0	0.0	52.0	0.0	0.1	35.5	1.0	4.5	3.69	12
Silver	Wisconsin	1932	3	37.5	0.0	62.5	0.0	0.0	0.0	0.0	0.0	3.88	12
Simcoe	Ontario	1927	9	4.0	0.0	22.0	0.0	0.0	74.0	0.0	0.0	3.91	27
Star	Wisconsin	1931	1	20.0	0.0	20.0	0.0	0.0	30.0	30.0	0.0	3.70	12
Trout	Wisconsin	1931	38	13.5	0.1	63.0	0.0	0.0	20.5	1.0	3.0	3.75	12
Trout	Wisconsin	1932	103	4.0	0.5	45.1	0.0	0.0	36.5	0.0	14.0	3.72	12
Vieux	Wisconsin	1932	2	0.0	0.0	24.0	0.0	0.0	0.0	0.0	76.0	3.50	12
Winona	Wisconsin	1940	10	26.6	0.0	9.5	18.0	7.1	37.3	0.0	0.0	3.98	11
Mean				10.0	3.0	42.2	2.8	1.7	31.2	2.1	6.4	3.74	
Smallmouth bass (total n = 3162 fish)													
11 lakes	Maine	1936–38	31	14.9	0.3	6.0	12.5	0.0	66.3	0.0	0.0	4.04	1
7 lakes	Maine	1940	66	80.3	0.0	3.6	0.0	0.0	14.4	1.7	0.0	4.37	44
8 lakes	Maine	1941	259	83.9	5.8	8.0	1.6	0.0	0.0	0.7	0.0	4.34	1
—	Michigan	1964	177	43.0	0.0	0.5	0.0	0.0	56.5	0.0	0.0	4.21	45
Bay de Noc (Michigan)	Michigan	1966–68	57	75.0	0.0	0.1	0.0	0.0	25.0	0.0	0.0	4.38	46
Bay de Noc (Michigan)	Michigan	1966–68	112	97.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	4.45	46
Bear	Wisconsin	1931	1	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.50	12
Cacapon R.	Virginia	1939	104	2.7	0.0	87.6	8.2	0.4	1.1	0.0	0.2	3.57	47
Cache	Ontario	1935-36	52	28.7	16.0	19.7	0.0	0.0	35.7	0.0	0.0	3.97	48
Clear	Wisconsin	1931	2	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.50	12
Crystal	Wisconsin	1931	4	0.0	0.0	97.5	0.0	0.0	0.0	3.5	0.0	3.50	12
Douglas	Michigan	1915	8	10.0	0.0	0.0	0.0	0.0	70.0	0.0	20.0	3.95	20
Erie	Ontario	1938	157	82.5	0.0	0.2	0.0	0.0	17.5	0.0	0.0	4.41	48
Genesee R.	New York	1927	13	18.4	0.0	24.2	0.0	0.0	56.0	0.0	0.0	3.94	20
Geneva	Wisconsin	1921	21	33.0	4.0	43.0	0.0	0.0	20.6	0.0	0.0	3.94	20
Georgian Bay	Ontario	1936	45	62.5	0.0	1.5	0.0	0.0	33.5	0.0	0.0	4.26	48
Georgian Bay	Ontario	1928	98	27.7	0.0	0.4	0.2	0.0	71.7	0.2	0.0	4.14	32
Illinois R.	Illinois	1880	10	5.0	0.0	35.0	0.0	0.0	60.0	0.0	0.0	3.85	20

Appendix I (*continued*).

			n	Prey category								Trophic	
Lake	Location	Year	fish	Fish	Zoop	Ben	Pred ben	Mol	Cray	Det	Other	position	Reference[a]
Juniala R.	Pennsylvania	1990	102	0.0	0.0	93.9	0.0	0.0	6.2	0.0	0.0	3.53	49
Jute	Wisconsin	1931	28	83.5	0.0	13.0	0.0	0.0	0.0	0.0	2.0	4.31	12
Kathenne	Michigan	1974	167	28.0	8.7	32.0	5.3	0.0	13.0	0.0	13.0	3.87	15
Larry	Wisconsin	1931	14	0.0	2.0	94.5	0.0	0.0	0.0	1.5	0.0	3.46	12
Memphremagog	Quebec	1973	24	50.1	0.0	3.2	0.0	0.0	50.0	0.0	0.0	4.30	50
Michigan	Wisconsin	1921	2	98.5	0.0	0.0	0.0	0.0	0.0	1.5	0.0	4.48	20
Monona	Wisconsin	1918	4	80.0	0.0	20.0	0.0	0.0	0.0	0.0	0.0	4.30	20
Muskellunge	Wisconsin	1931	57	75.0	0.0	12.0	0.0	1.0	0.0	11.0	1.0	4.19	12
Muskellunge	Wisconsin	1932	61	42.0	1.5	48.5	0.0	0.0	0.0	6.5	2.0	3.90	12
Nebish	Wisconsin	1931	66	20.5	12.0	62.0	0.0	1.5	0.0	0.0	3.0	3.68	12
Nebish	Wisconsin	1932	42	41.0	0.0	56.5	0.0	0.0	0.1	0.0	2.0	3.90	12
Nebish	Wisconsin	1977	101	7.2	0.0	3.2	5.4	0.0	84.2	0.0	0.0	4.02	24
Nebish	Wisconsin	1978	126	22.0	0.3	11.0	2.9	0.0	64.0	0.0	0.0	4.06	24
Nebish	Wisconsin	1979	104	15.5	0.1	8.8	5.8	0.0	69.9	0.0	0.0	4.04	24
Nebish	Wisconsin	1980	125	10.0	0.0	3.4	4.1	0.0	82.6	0.0	0.0	4.04	24
Nebish	Wisconsin	1981	111	8.9	0.1	7.2	4.4	0.0	80.1	0.0	0.0	4.02	24
Nipigon	Ontario	1921	9	48.0	35.3	16.6	0.0	0.0	0.0	0.0	0.0	3.98	25
Nipissing	Ontario	1929	106	20.6	0.0	0.4	0.0	0.0	79.0	0.0	0.0	4.10	32
Opeongo	Ontario	1936	91	9.7	0.0	2.3	0.0	0.0	87.0	0.0	0.0	4.02	48
Oxtongue R.	Ontario	1930	6	20.0	0.0	80.0	0.0	0.0	0.0	0.0	0.0	3.70	32
Ozark streams	Arkansas	1980	74	34.0	0.0	6.0	0.0	0.0	60.0	0.0	0.0	4.14	34
Pallette	Wisconsin	1931	16	58.5	1.5	40.0	0.0	0.0	0.0	0.0	0.0	4.09	12
Pallette	Wisconsin	1932	30	58.5	2.5	35.5	0.0	0.0	0.0	1.5	9.5	4.09	12
Pepin	Wisconsin	1921	12	56.5	5.7	29.8	0.0	0.0	9.1	0.0	0.0	4.13	20
Perch	Ontario	1930–31	123	49.7	1.7	5.3	0.1	0.0	39.2	0.2	3.9	4.19	32
Phantom	Ontario	1930	18	4.0	0.0	22.6	0.0	0.0	71.7	1.7	0.0	3.89	32
Potomac	Virginia	1939	96	4.1	0.0	94.6	0.5	0.1	0.6	0.0	0.1	3.55	47
Razor	Wisconsin	1931	18	39.5	2.0	53.0	0.0	0.0	0.0	0.0	6.0	3.90	12
Rock	Wisconsin	1931	6	5.0	0.0	88.5	0.0	0.0	0.0	5.5	1.0	3.52	12
Shenandoah R.	Virginia	1939	108	37.3	0.0	49.8	8.1	0.0	4.3	0.0	0.5	3.93	47
Silver	Wisconsin	1931	31	35.0	0.0	55.0	0.0	0.0	9.5	1.0	0.0	3.90	12
Silver	Wisconsin	1932	5	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.50	12
Simcoe	Ontario	1927	16	29.0	0.0	7.0	8.0	3.0	53.0	0.0	0.0	4.08	27
Spider	Wisconsin	1931	3	0.0	0.0	27.0	0.0	0.0	15.5	0.0	58.0	3.59	12
Star	Wisconsin	1931	1	0.0	0.0	50.0	0.0	0.0	50.0	0.0	0.0	3.75	12
Trout	Wisconsin	1931	10	0.0	7.0	89.5	0.0	0.0	0.0	0.0	4.5	3.52	12
Trout	Wisconsin	1932	1	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	4.00	12
Weber	Wisconsin	1931	29	6.0	5.0	76.0	0.0	0.0	0.0	1.0	14.0	3.59	12
Weber	Wisconsin	1932	2	83.0	0.0	17.0	0.0	0.0	0.0	0.0	0.0	4.33	12
Mean				37.6	2.0	28.8	1.2	0.1	27.3	0.7	2.3	4.02	
Largemouth bass (total n = 5664 fish)													
Bear	Wisconsin	1931	5	80.0	0.0	20.0	0.0	0.0	0.0	0.0	0.0	4.30	12
Cub	Michigan	1974	340	54.3	0.0	0.0	11.0	0.0	0.0	0.0	35.0	4.10	15
Deer Island	—	1973	169	53.4	0.4	19.6	0.0	0.0	14.9	0.1	11.9	4.11	35
DeGray	Arkansas	1976	748	59.0	0.0	0.3	0.0	0.0	37.6	0.5	3.0	4.28	36
Fork	—	1941		48.0	0.0	18.2	11.0	0.0	113	0.0	11.0	4.08	37
Geneva	Wisconsin	1918	78	8.7	18.1	48.1	0.0	0.0	0.0	0.0	25.0	3.59	20
L. Dixie	Missouri	1964	900	50.1	0.0	1.5	0.7	0.0	39.	0.6	6.3	4.18	38
Long	Wisconsin	1931	3	50.0	0.0	4.0	0.0	0.0	0.0	0.0	46.0	4.00	12
Maple	Minnesota	1957	83	96.0	3.0	0.0	0.0	0.0	0.0	1.0	0.0	4.46	7
Murphy Flowage	Wisconsin	1961–64	1146	33.5	0.0	1.2	0.0	0.0	56.1	6.1	0.0	4.04	39
Muskellunge	Wisconsin	1931	19	50.5	32.0	9.5	0.0	0.0	0.0	1.5	7.5	4.01	12
Muskellunge	Wisconsin	1932	8	94.0	0.0	0.0	0.0	0.0	0.0	6.0	0.0	4.41	
Opinicon	Ontario	1991	10	85.7	1.8	0.0	0.0	0.0	11.4	0.0	0.0	4.40	2
Paul	Michigan	1987	235	42.0	11.0	8.0	39.0	0.0	0.0	0.0	0.0	4.12	40
Paul	Michigan	1988		55.0	10.0	14.0	21.0	0.0	0.0	0.0	0.0	4.16	40

Appendix I (*continued*).

Lake	Location	Year	*n*	Prey category								Trophic	Reference^a
			fish	Fish	Zoop	Ben	Pred ben	Mol	Cray	Det	Other	position	
Peter	Michigan	1987	235	0.0	6.5	45.6	46.5	0.8	0.0	0.0	0.0	3.72	41
Peter	Michigan	1988	235	54.0	6.0	8.0	32.0	0.0	0.0	0.0	0.0	4.20	40
Peter	Michigan	1987		0.0	15.0	15.0	35.0	0.0	0.0	0.0	35.0	3.68	40
Shelbyville	Illinois	1980	97	99.2	0.0	0.8	0.0	0.0	0.0	0.0	0.0	4.49	42
Shelbyville	Illinois	1978–81	1347	88.8	0.0	0.6	0.0	0.0	11.4	0.0	0.0	4.46	43
Winona	Wisconsin	1940	6	17.6	0.0	16.9	0.0	0.0	40.5	25.0	0.0	3.75	11
Mean				53.3	4.9	11.0	9.3	0.0	10.6	1.9	8.6	4.12	
Northern pike and chain pickerel (total *n* = 34 738 fish)													
19 lakes	Maine	1940	110	94.8	0.0	0.2	0.0	0.0	0.5	0.0	4.4	4.37	44
20 lakes	Maine	1937–41	95	95.1	0.0	0.0	0.1	0.0	0.0	0.0	4.8	4.24	1
Babcock Pond	Connecticut	1941	71	91.4	0.0	0.0	3.7	0.0	0.0	0.0	4.8	4.04	
Bay de Noc (Michigan)	Michigan	1966–68	405	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.36	
Bay of Ouinte (Ontario)	Ontario	1958–64	131	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.55	74
Brochet	Quebec	1953	131	40.2	0.0	9.3	32.1	0.0	18.4	0.0	0.0	4.15	52
Cree	Saskatchewan	1955	—	95.0	0.0	0.0	5.0	0.0	0.0	0.0	0.0	4.48	53
Georgian Bay (Huron)	Ontario	1928	11	53.8	0.0	0.0	0.0	0.0	46.2	0.0	0.0	4.27	32
Grande Rivière	Quebec	1977		97.9	0.0	0.3	0.0	0.0	0.0	0.0	1.8	4.48	52
Great Slave	N.W.T.	1944–47	73	95.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	4.45	54
Grove	Minnesota	1957	133	90.0	0.0	0.0	0.0	0.0	0.0	0.0	10.0	4.40	7
Heming	Manitoba	1950–62	29477	99.9	0.0	0.1	0.0	0.0	0.1	0.0	0.0	4.42	55
Keller	N.W.T.	1962	125	97.2	0.0	0.0	2.8	0.0	0.0	0.0	0.0	4.59	56
Lincoln Pond	New York	39	145	32.8	1.4	47.4	17.6	0.0	0.0	0.0	0.8	3.72	
Maple	Minnesota	1957	70	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.50	7
Mecan R.	Wisconsin	1959	91	95.9	0.0	0.0	0.0	0.0	1.5	0.0	2.6	4.31	58
Memphremagog	Quebec	1973	27	60.0	0.0	2.1	0.0	0.0	40.0	0.0	0.0	4.09	50
Mississippi	Mississippi	1968	58	96.5	0.0	0.0	0.0	0.0	3.5	0.0	0.0	4.36	59
Monroe	Quebec	1953	221	99.5	0.0	0.1	0.1	0.0	0.3	0.0	0.0	4.50	52
Murphy Flowage	Wisconsin	1965	1412	99.1	0.0	0.0	0.0	0.0	0.2	0.0	0.0	4.29	39
Nipigon	Ontario	1921	23	95.2	0.7	0.7	0.0	0.0	0.0	0.0	3.8	4.46	26
Nipissing	Ontario	1929–30	10	36.3	0.0	0.0	0.0	0.0	59.4	0.0	4.0	4.15	32
Ontario	New York	1972	87	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.02	61
Pocotopaug	Connecticut	—	30	63.0	0.0	11.0	11.0	0.0	8.0	4.0	4.0	4.19	76
Various	—	—	—	64.0	0.0	22.0	0.0	0.0	12.0	1.0	1.0	3.82	76
Seney Refuge	Michigan	1941–42	378	69.5	0.0	1.8	0.9	0.1	23.1	0.0	4.6	4.31	2
Seney Refuge	Michigan	1952	84	65.4	0.0	0.1	2.5	0.1	21.4	0.0	10.6	4.28	2
Simcoe	Ontario	1982	50	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.49	62
Ste. Anne	Alberta	1976–78	1290	99.5	0.0	0.5	0.0	0.0	0.0	0.0	0.0	4.50	63
Wollaston	Saskatchewan	1956	—	95.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	4.45	53
Mean				84.1	0.1	3.5	2.5	0.0	7.8	0.2	1.9	4.31	
Walleye (total *n* = 10 386 fish)													
Bay de Noc (Michigan)	Michigan	1966–68	103	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.39	46
Bay of Ouinte (Ontario)	Ontario	1958–62	692	99.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	4.04	74
Clear	Wisconsin	1931	15	60.0	12.0	19.5	0.0	0.0	0.0	4.5	5.0	4.06	12
Clear	Wisconsin	1932	23	40.5	0.0	59.5	0.0	0.0	0.0	0.0	0.5	3.92	12
Erie	Ontario	1979–81	906	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.50	64
Falcon	Manitoba	1959	288	92.2	0.0	5.5	0.0	0.0	3.0	0.0	0.0	4.48	45
Great Slave	N.W.T.	1944–47	116	75.0	0.0	25.0	0.0	0.0	0.0	0.0	0.0	4.25	54
James Bay	Quebec	1979	584	72.3	1.3	24.0	2.4	0.0	0.0	0.0	0.0	4.24	65
Lac la Ronge	Saskatchewan	1948–55	276	97.0	0.0	2.8	0.0	0.0	0.3	0.0	0.0	4.35	66
Lake of the Woods	Ontario	1968–70	1417	98.8	0.3	1.3	0.0	0.0	0.0	0.0	0.0	4.61	67
Lake of the Woods	Ontario	1968–70	1605	88.0	1.5	11.3	0.0	0.0	1.8	0.0	0.0	4.49	67
Lost	Wisconsin	1932	18	99.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	4.50	12
Memphremagog	Quebec	1973	8	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.70	50
Nipigon	Ontario	1920–21	74	91.1	0.0	6.6	0.0	0.0	0.0	0.0	0.0	4.35	25
Nipigon	Ontario	1921	4	50.0	47.4	2.5	0.0	0.0	0.0	0.0	0.0	4.00	26

Appendix I (*concluded*).

Lake	Location	Year	n fish	Prey category								Trophic position	Reference[a]
				Fish	Zoop	Ben	Pred ben	Mol	Cray	Det	Other		
Nipissing	Ontario	1929–30	16	48.3	0.0	28.1	0.0	0.0	22.9	0.0	0.0	4.08	32
Oahe	South Dakota	1993	478	99.6	0.0	0.4	0.0	0.0	0.0	0.0	0.0	4 50	68
Ontario	Michigan	1966–68	103	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.50	46
Pike	Minnesota	1962	470	43.2	0.0	26.5	9.3	0.0	18.0	3.0	0.0	4.11	72
Simcoe	Ontario	1982	50	100.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.57	62
Sparkling	Wisconsin	1982–83	113	97.8	0.0	2.2	0.0	0.0	0.0	0.0	0.0	4.42	69
Trout	Wisconsin	1931	30	96.0	0.0	1.0	0.0	0.0	0.0	0.0	2.5	4.45	12
Trout	Wisconsin	1932	22	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.50	12
West Blue	Manitoba	1970	79	79.8	0.0	9.3	0.0	0.0	11.0	0.0	0.0	4.51	70
West Blue	Manitoba	1966	—	78.0	0.0	4.2	0.6	0.0	15.6	0.0	1.5	4.53	75
West Blue	Manitoba	1969–70	—	71.5	0.0	16.9	5.0	0.0	4.8	0.0	1.9	4.43	75
Wilson	Minnesota	1964–65	390	70.7	0.0	27.6	0.0	0.0	0.0	0.0	1.7	4.19	73
Wilson	Minnesota	67–70	230	41.4	0.0	44.4	0.0	0.0	2.1	0.0	12.1	3.88	73
Winnebago	Wisconsin	1960	1148	99.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	4.43	71
Winnebago	Wisconsin	1960	629	99.7	0.0	0.3	0.0	0.0	0.0	0.0	0.0	4.26	71
Winnebago	Wisconsin	1961	56	95.4	0.4	4.6	0.0	0.0	0.0	0.0	0.0	4.26	71
Winnebago	Wisconsin	1961	231	81.6	0.0	18.4	0.0	0.0	0.0	0.0	0.0	4.10	71
Mean				83.3	2.0	10.7	0.5	0.0	2.5	0.2	0.8	4.33	

Note: Dietary data are broken down into the prey categories described in Table 1. The summary presented at the end of each species represents the mean diet and trophic position for the species.

[a](1) Cooper 1942; (2) Lagler 1956; (3) Laughlin and Werner 1980; (4) Fox and Keast 1990; (5) Snetsinger 1992; (6) Etnier 1971; (7) Seaburg and Moyle 1964; (8) Keast and Welsh 1968; (9) Sadzikowski and Wallace 1976; (10) Flemer and Woolcott 1966; (11) Parks 1949; (12) Couey 1935; (13) Boisclair 1988; (14) Moffett and Hunt 1943; (15) Clady 1974; (16) Griswold and Tubb 1977; (17) Parrish and Margraf 1990; (18) Parrish and Margraf 1994; (19) Schaeffer and Margraf 1986; (20) Adams and Hankinson 1928; (21) Hunt and Carbin 1950; (22) Tharratt 1959; (23) Fraser 1978; (24) Serns and Hoff 1984; (25) Clemens et al. 1923; (26) Clemens et al. 1924; (27) Rawson 1930; (28) Mills and Forney 1981; (29) Keast 1977; (30) Weisberg and Janicki 1990; (31) Ward and Robinson 1974; (32) Tester 1932; (33) Vadas 1990; (34) Probst et al. 1984; (35) Saiki and Tash 1978; (36) Bryant and Moen 1980; (37) Bennett 1948; (38) Herman et al. 1969; (39) Snow 1971; (40) Hodgson et al. 1991; (41) Hodgson et al. 1989; (42) Miller and Storck 1984; (43) Storck 1986; (44) Cooper 1941; (45) Fedoruk 1966; (46) Wagner 1972; (47) Surber 1941; (48) Doan 1940; (49) Johnson and Dropkin 1995; (50) Nakashima and Leggett 1975; (51) Foote and Blake 1945; (52) Vallieres and Fortin 1988; (53) Rawson 1959; (54) Rawson 1951; (55) Lawler 1965; (56) Johnson 1972; (57) Raney 1942; (58) Hunt 1965; (59) McIlwain 1970; (61) Wolfert and Miller 1978; (62) Mathers and Johansen 1985; (63) Diana 1979; (64) Knight et al. 1984; (65) Hazel and Fortin 1986; (66) Rawson 1965; (67) Swenson and Smith 1976; (68) Bryan et al. 1995; (69) Lyons and Magnuson 1987; (70) Kelso 1973; (71) Priegel 1963; (72) Johnson and Hale 1977; (73) Johnson 1977; (74) Hurley and Christie 1977; (75) Kelso and Ward 1977; (76) Hunter and Rankin 1939.

Appendix II. Diets of northern pike, chain pickeral, and walleye in lakes where fish prey items could be further separated into species.

Lake	Location	Year	*n* fish	% fish	% volume														Trophic position	Reference[a]
					Perc.	Cypr.	Cent.	Trpe.	Cato.	Scul.	Alew.	Smel.	Core.	Salm.	Burb.	Stic.	Wb.	Other		
					Northern pike and chain pickerel (total *n* = 32 284 fish)															
19 lakes	Maine	1940	110	94.8	7.9	14.6	0.0	0.0	0.0	0.0	0.0	3.2	0.0	0.0	0.0	0.0	58.0	11.2	4.37	44
20 lakes	Maine	1937–41	95	95.1	19.4	22.5	1.0	0.0	0.0	0.0	0.0	1.0	0.0	24.5	0.0	0.0	25.6	1.0	4.24	1
Babcock Pond	Connecticut	1941	71	91.4	0.0	42.4	5.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	43.7	4.04	51
Bay de Noc	Michigan	1966–68	405	100.0	2.8	7.0	4.6	10.7	0.0	0.0	34.2	39.1	0.0	0.0	0.0	0.0	0.0	1.6	4.36	46
Bay of Quinte	Ontario	1958–64	131	100.0	53.2	0.0	2.0	21.8	0.0	0.0	19.9	3.1	0.0	0.0	0.0	0.0	0.0	0.0	4.55	75
Heming	Manitoba	1950–62	29477	99.9	22.5	19.8	0.0	34.4	12.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.3	4.42	55
Keller	N.W.T.	1962	125	97.2	0.0	0.0	0.0	0.0	5.7	28.6	0.0	0.0	0.0	0.0	37.2	22.9	0.0	2.9	4.59	56
Lincoln Pond	New York	1939	145	32.8	0.0	17.4	15.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.72	57
Mecan River	Wisconsin	1959	91	95.9	0.0	4.6	0.0	0.0	9.0	22.8	0.0	0.0	0.0	59.6	0.0	0.0	0.0	0.0	4.31	58
Memphremagog	Quebec	1973	27	60.0	30.0	30.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.09	50
Mississippi	Mississippi	1968	58	96.5	0.0	0.0	59.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	36.6	4.36	59
Murphy Flowage	Wisconsin	1965	1412	99.1	13.8	6.0	77.7	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	1.4	4.29	39
Ontario	New York	1972	87	100.0	2.3	0.0	0.0	0.0	0.0	0.0	97.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.02	61
Various	—	—	—	64.0	12.6	41.0	2.3	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.5	3.82	77
Simcoe	Ontario	1982	50	100.0	28.4	1.5	4.9	1.6	35.3	0.0	0.0	8.0	20.2	0.0	0.0	0.0	0.0	0.0	4.49	62
Mean				88.4	12.9	13.8	11.5	4.6	4.2	3.4	10.1	3.6	1.3	5.6	2.5	1.5	5.6	7.7	4.24	
					Walleye (total *n* = 8369 fish)															
Bay de Noc	Michigan	1966–68	103	100.0	0.0	0.0	0.0	0.0	8.8	0.0	37.3	40.1	0.0	0.0	0.0	0.0	0.0	13.8	4.39	46
Bay of Quinte	Ontario	1958–62	692	99.0	0.4	0.0	0.0	0.0	0.0	0.0	94.6	4.0	0.0	0.0	0.0	0.0	0.0	0.0	4.04	75
Falcon	Manitoba	1959	288	92.2	49.5	6.2	8.4	2.2	12.4	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.4	4.48	45
James Bay	Quebec	1979	584	72.3	0.0	0.0	0.0	41.1	0.0	0.0	0.0	0.0	26.6	0.0	4.5	0.0	0.0	0.0	4.24	65
Lac la Ronge	Saskatchewan	1948–55	276	97.0	1.0	2.0	0.0	31.0	7.0	0.0	0.0	0.0	56.0	0.0	0.0	0.0	0.0	0.0	4.35	66
Lake of the Woods	Ontario	1968–70	1417	98.8	30.0	3.3	0.0	53.7	0.0	0.0	0.0	0.0	6.1	0.0	0.0	0.0	0.0	5.6	4.61	67
Lake of the Woods	Ontario	1968–70	1605	88.0	72.8	9.5	0.0	5.1	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	4.49	67
Memphremagog	Quebec	1973	8	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	4.70	50
Pike	Minnesota	1962	470	43.2	27.4	0.1	0.0	0.5	13.3	1.3	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	4.11	73
Simcoe	Ontario	1982	50	100.1	19.4	11.0	0.0	1.0	0.0	0.0	0.0	68.7	0.0	0.0	0.0	0.0	0.0	0.0	4.57	62
Sparkling	Wisconsin	1982–83	113	97.8	69.2	19.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.5	0.0	0.0	0.0	4.42	69
West Blue	Manitoba	1970	79	79.8	71.0	0.0	0.0	8.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.51	70
West Blue	Manitoba	1966	—	78.0	77.2	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.53	76
West Blue	Manitoba	1969–70	—	71.5	63.9	0.0	0.0	7.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.43	76
Wilson	Minnesota	1964–65	390	70.7	55.8	14.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.19	74
Wilson	Minnesota	1967–70	230	41.4	20.6	20.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.88	74
Winnebago	Wisconsin	1960	1148	99.0	19.9	10.9	2.6	8.9	0.0	0.0	0.0	0.0	0.0	0.0	4.1	0.0	0.0	52.6	4.43	71
Winnebago	Wisconsin	1960	629	99.7	0.0	34.3	7.1	58.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.26	71
Winnebago	Wisconsin	1961	56	95.4	0.0	1.6	93.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.26	71
Winnebago	Wisconsin	1961	231	81.6	0.0	16.1	47.0	18.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.10	71
Mean				85.3	28.9	7.5	7.9	11.9	2.1	0.1	6.6	10.6	4.5	0.0	0.9	0.0	0.0	4.2	4.35	

Note: Perc., yellow perch; Cypr., cyprinids; Cent., centrarchids; Trpe., trout-perch; Cato., catostomids; Scul., sculpins; Alew., alewife; Smel., smelt; Core., coregonids; Salm., salmoninae; Burb., burbot; Stic., sticklebacks; Wb., white bass; Other, nonspecified species.

[a] See footnote *a* to Appendix I.

Appendix III. Estimated trophic position of adult littoral fish species based on $\delta^{15}N$ from 36 lakes in Ontario and Quebec.

Lake	$\delta^{15}N$ Unionid mussel	Trophic position						
		Pump.	Perc.	Rb.	Smb.	Lmb.	Pike	Wall.
Ahmic	5.3	—	3.92	3.84	—	—	3.53	4.24
Balsam	4.1	3.45	3.73	3.65	—	—	—	—
Bernard	3.1	—	—	—	3.55	—	—	—
Big Rideau	4.7	3.23	2.99	—	—	—	3.82	—
Brandy	3.9	3.83	3.42	3.77	3.91	—	3.78	—
Buck	3.8	3.53	3.56	—	4.16	4.03	3.63	—
Carson	1.6	—	—	—	3.94	4.41	—	—
Christie	4.4	—	3..77	—	—	—	4.18	4.10
Clear	5.7	—	3.39	—	—	—	4.02	—
Cameron	4.5	2.81	3.50	3.45	—	—	—	—
Constan	3.3	—	—	—	—	—	3.38	—
Crotch	4.1	—	3.46	—	3.73	3.87	3.77	—
Dalrymple	6.0	3.14	—	—	3.89	—	4.02	—
Doe	4.7	3.36	3.73	3.96	3.87	—	3.59	—
Doré	5.1	3.45	3.34	3.92	3.91	—	4.41	—
Fox	4.2	3.68	—	—	—	4.13	3.73	—
Gloucester Pool	3.7	—	3.90	—	—	—	4.08	4.55
Golden	3.1	—	4.00	—	4.20	—	4.08	4.55
Hurds	3.2	3.45	4.25	4.04	—	4.18	4.31	—
Kashagawigamog	4.8	—	3.87	3.45	—	—	—	—
Kennisis	2.3	—	4.33	—	—	—	—	—
Mazinaw	1.3	4.15	3.76	4.43	4.73	—	3.69	4.86
Memphremagog	7.6	—	3.16	—	—	—	—	—
Memesagamesing	4.3	—	—	—	—	—	3.80	—
Mississippi	3.9	3.68	3.69	3.86	—	3.92	—	4.30
Oak	4.9	2.93	3.11	—	3.57	—	—	—
Obabika	3.9	—	3.52	—	—	—	3.49	—
Pickerel	4.2	3.05	3.42	—	—	4.02	3.57	4.53
Peninsula	3.3	—	—	—	4.63	—	—	—
Rice	7.3	—	3.34	3.76	—	—	—	4.09
Robertson	4.0	3.54	3.46	4.17	3.79	—	4.51	—
Round	5.4	3.18	3.40	—	4.17	—	—	4.48
Sand	3.9	—	4.07	—	—	—	—	—
Stenburg	3.9	3.21	3.43	3.81	4.18	—	—	—
Sturgeon	4.8	3.11	3.65	4.09	—	—	—	4.29
Wollaston	4.3	3.52	—	—	—	—	—	—

Note: Pump., pumpkinseed; Perc., yellow perch; Rb., rock bass; Smb., smallmouth bass; Lmb., largemouth bass; Pike, northern pike and chain pickerel; Wall., walleye.

Changes in size at maturity of Fraser River sockeye salmon (*Oncorhynchus nerka*) (1952–1993) and associations with temperature

Sean P. Cox and Scott G. Hinch

Abstract: Unlike other Canadian Pacific salmon (*Oncorhynchus* spp.), long-term declines in the size at maturity of Fraser River sockeye salmon (*O. nerka*) have not been reported in past studies. Using data specific for 10 Fraser River sockeye stocks, we demonstrate that size at maturity has generally declined over the past 42 yr for females in all stocks and for males from eight stocks. Independent of this temporal trend, we found that size at maturity of both sexes in all stocks was smaller in years when sea surface temperatures were relatively warm. Slower growth in warmer years may be caused directly by increased metabolic demand, or indirectly by oceanic changes that influence food acquisition. We speculate that fitness of Fraser River sockeye will be reduced in the future if sea surface temperature increases and salmon abundance remains near present levels.

Résumé : Contrairement à d'autres saumons du Pacifique (*Oncorhynchus* spp.) canadiens, on n'a pas signalé dans les études antérieures de déclin à long terme de la taille à maturité du saumon sockeye (*O. nerka*) du fleuve Fraser. Nous avons démontré, à l'aide des données spécifiques de 10 stocks de saumon sockeye du fleuve Fraser, que la taille à maturité a décliné de façon générale au cours des 42 dernières années dans tous les stocks pour ce qui est des femelles et dans huit stocks pour ce qui est des mâles. Indépendamment de cette tendance temporelle, nous avons constaté que la taille à maturité des deux sexes dans tous les stocks était plus faible au cours des années où la température de la surface de la mer était relativement chaude. Une croissance plus lente au cours des années plus chaudes peut être causée directement par une augmentation de la demande métabolique ou indirectement par des changements dans l'océan qui influent sur l'acquisition des aliments. Nous estimons que l'aptitude physique du saumon sockeye du fleuve Fraser sera réduite dans l'avenir si la température de la surface de la mer augmente et si l'abondance du saumon reste proche des valeurs actuelles.

[Traduit par la Rédaction]

Introduction

The size at maturity of Pacific salmon (*Oncorhynchus* spp.) has been decreasing in recent decades (Ricker 1982, 1995; Ogura et al. 1991; Helle and Hoffman 1995; Ishida et al. 1995). From 1951 to 1975, average weight of adult pink (*O. gorbuscha*), coho (*O. kisutch*), and chinook salmon (*O. tshawytscha*) caught in coastal waters of British Columbia decreased by 5–25% (Ricker 1995). This reduction in weight has slowed somewhat for chinook salmon in recent years; however, declines in weight of pink and coho salmon have continued (Ricker 1995). Declines of similar magnitudes have been observed for adult chum salmon (*O. keta*) captured in Asian and Alaskan waters (Ogura et al. 1991; Helle and Hoffman 1995).

Sockeye salmon (*O. nerka*) are the second most abundant salmon species in British Columbia waters and the most economically valuable (Healey 1993). Unlike other species, long-term declines in length or weight at maturity of Canadian sockeye salmon have not been detected (Ricker 1995). One reason may be that mixed-stock commercial catch data obscure individual stock trends. Age and size at maturity of Fraser River sockeye salmon can vary substantially among breeding populations (stocks), a result of both oceanic and genetic factors (Healey 1986; Blackbourn 1987; Burgner 1991). Our first objective was to determine if stock-specific time trends exist for Fraser River sockeye salmon, and whether some or all of them are consistent with those of other Pacific salmon. We focus on Fraser River sockeye stocks.

The ocean life history of Fraser River sockeye salmon is typical of most British Columbia sockeye. In their second year of life, they enter the ocean and move northward along the coast between April and June (Groot et al. 1989; Burgner 1991). During autumn, they move offshore into the open waters of the Gulf of Alaska where they typically remain for 2 yr before maturing and returning to the Fraser River in their fourth year (French et al. 1976). Considerable among-year variation in size at maturity exists within most sockeye stocks (Healey 1986). Because size at maturity is not related to smolt size (Henderson and Cass 1991), oceanic environmental conditions must be largely responsible for variation in size at maturity.

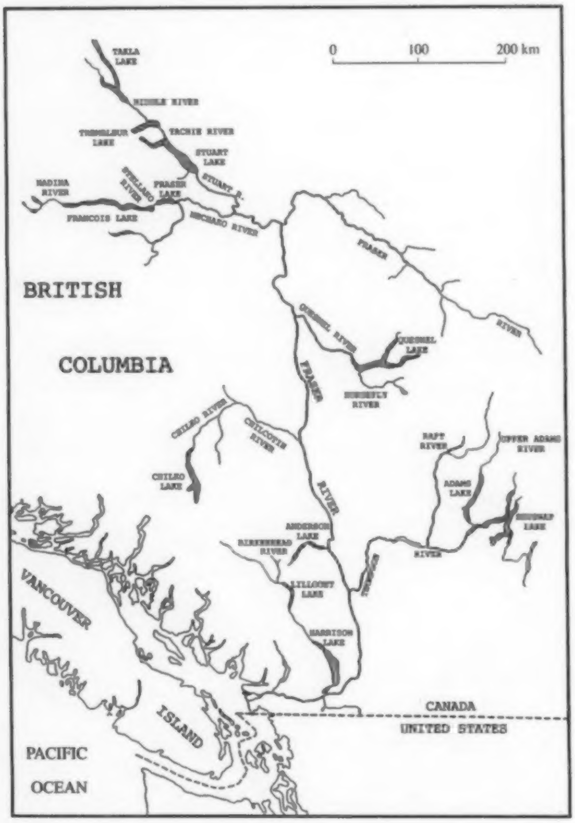
One of the main factors that may be responsible for interannual changes in size at maturity is temperature. Temperature affects growth directly through changes to metabolic costs (Nikolsky 1963; Furnell and Brett 1986; Jobling 1994; Hinch et al. 1995*a*), or indirectly through alteration of features that affect food acquisition (e.g., high-seas distribution, population density, or migration routes; Ricker 1982; Laevastu 1984; Blackbourn 1987; Hsieh et al. 1991; Ishida et al. 1995; Welch

Received January 30, 1996. Accepted October 7, 1996.
J13279

S.P. Cox.[1] Fisheries Centre and Department of Earth and Ocean Sciences, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.
S.G. Hinch. Institute for Resources and Environment and Department of Forest Sciences, University of British Columbia, Vancouver, BC V6T 1Z2, Canada.

[1] Author to whom all correspondence should be addressed.

Fig. 1. Map of the major sockeye salmon spawning rivers and rearing lakes of the Fraser River watershed (adapted from Killick and Clemens 1963).



et al. 1995). Hinch et al. (1995*a*, 1995*b*) found a negative relationship between sea surface temperature (SST) and size at maturity of Early Stuart sockeye salmon, a relatively small Fraser stock; however, these results may be too specific to a single stock to be generally applicable to Fraser River sockeye as a whole. Ricker (1982) found associations between SST and size of Fraser River sockeye salmon using mixed-stock commercial catch data collected from 1951 to 1974. However, SST regimes in the North Pacific Ocean have changed dramatically since 1974 (Hourston 1992), so SST–size correlations may also have changed; another problem is that mixed-stock data may obscure or bias general species relationships between size at maturity and environmental factors if a small number of stocks have a dominant influence. Our second objective was to examine the associations between SST and size at maturity of Fraser River sockeye salmon using stock-specific information.

Methods

Size at maturity and SST data

As a measure of size at maturity, we used the average lengths of sockeye salmon measured on the major spawning grounds in the Fraser River drainage (Fig. 1). Although weight may be the best measure of size, large losses in weight occur during the up-river spawning migrations. Length changes very little during this migration, so it is a better measure of size when dealing with spawning ground data. Average standard lengths (SL) of male and female age 4_2 sockeye from the spawning grounds of the Adams, Horsefly, Chilko, Early Stuart, Late Stuart, Raft, Late Nadina, Stellako, Birkenhead, and Gates stocks were obtained from the archives of the Canadian Department of Fisheries and Oceans and the Pacific Salmon Commission for the years 1952–1993, inclusive. The 4_2 age class accounts for up to 95% of Fraser River sockeye production in most years (Gable and Cox-Rogers 1993). The ages of spawning ground samples were determined by scales from 1952 to 1968 and by otoliths from 1968 to 1993 (M. Lapointe, Pacific Salmon Commission, Vancouver, B.C., personal communication).

There was considerable variation in the number of fish sampled for length on the spawning grounds. To ensure that average SL values from low sample years did not unduly affect results of analyses, we excluded years in which we did not have at least 20 SL values to create a mean for each combination of stock and sex. This criterion was chosen because of a natural gap in the data; in most years, numbers of samples were well in excess of 20, but in a few years the samples were less than 10. After excluding some data, annual sample sizes ranged from 72 to >500, depending on the stock (Table 1). A summary of stock- and sex-specific mean SL is presented in Table 2.

SST data came from the Comprehensive Ocean–Atmospheric Dataset which is described in Woodruff et al. (1987). Annual SST values were calculated by averaging the mean monthly SSTs for the region bounded by 142–146°W and 52–56°N. This geographic region was selected because it reflects the general area of the Gulf of Alaska that Fraser River sockeye inhabit (French et al. 1976). We used only January–July monthly temperatures because this period represents a portion of sockeye's life history that is halfway through their ocean residency when they are probably largely in the area where SST was estimated. In order to assess associations between SST encountered during their high-seas residency and SL at maturity, SST data were lagged by 1 yr before carrying out any statistical analyses.

Statistical analyses

Long-term trends in SL were determined by regressing SL on year (PROC REG, SAS Institute 1988). Among-stock regressions were compared using analysis of covariance (ANCOVA) with stock as the class variable (PROC GLM, SAS Institute 1988). ANCOVA was carried out separately for males and females. The presence of a long-term trend in SST was assessed by regressing SST on year.

In order to examine the influence of within-year variability in SL on among-year trends, we performed within-stock power analyses on each sex and determined among-year minimum detectable differences (MDD) in mean SL (Zar 1984). MDD reflect an estimate of measurement error. Stock- and sex-specific MDD were calculated using the mean sample size from each spawning area (1952–1993, inclusive) and the mean square errors (MSE) of length at maturity (1984–1993, inclusive). Only mean SL and sample size were available from the data archives prior to 1984. We used the MDD as a check on the statistical significance of sex- and stock-specific SL versus year relationships.

We removed existing linear time trends before relationships between SL and SST were determined in order to reduce spurious correlations caused by similar underlying time trends. Residuals from the stock- and sex-specific regressions of SL and SST on year were then regressed on each other to examine potential effects of temperature on size at maturity. To assess the generality of these relationships, among-stock regressions were compared using ANCOVA separately for each sex.

Results and discussion

Time trends

The slopes of the regressions of SL on year did not differ

Table 1. Mean and range of sample sizes used to determine within-year standard lengths for each stock over the period 1952–1993, inclusive.

	Females				Males			
Stock	Mean	Range	MSE	MDD	Mean	Range	MSE	MDD
Adams	142	20–513	4.11	0.68	108	35–337	4.82	0.83
Birkenhead	229	39–543	5.25	0.57	102	20–314	16.32	1.56
Chilko	253	32–587	3.98	0.49	113	35–226	5.42	0.83
Early Stuart	106	28–203	4.25	0.78	72	24–145	5.16	1.01
Gate	141	29–236	4.81	0.73	103	22–229	7.47	1.09
Horsefly	134	21–408	4.59	0.73	105	22–254	3.96	0.91
Late Nadina	135	20–290	4.17	0.71	93	20–228	4.63	0.89
Late Stuart	98	20–200	4.31	0.88	91	20–420	6.54	1.12
Raft	143	20–491	4.29	0.71	78	20–118	4.56	0.87
Stellako	164	79–314	5.08	0.67	118	34–299	5.42	0.83

Note: Mean square error (MSE, cm^2) of length at maturity and minimum detectable difference (MDD, cm) in among-year comparisons are based on data from 1984 to 1993, inclusive.

Table 2. Annual mean standard length at maturity (cm), SD, and number of years of data (*n*) for age 4_2 sockeye salmon stocks of the Fraser River.

	Females					Males				
Stock	Mean	SD	*n*	*r*	*P*	Mean	SD	*n*	*r*	*P*
Adams	54.12	1.32	38	–0.35	0.03	58.61	1.74	36	–0.39	0.02
Birkenhead	53.11	1.50	38	–0.35	0.03	54.32	2.44	37	0.20	0.21
Chilko	52.29	1.61	41	–0.55	<0.01	54.98	1.47	41	–0.37	0.01
Early Stuart	52.80	1.31	33	–0.62	<0.01	55.73	1.12	31	–0.41	0.01
Gates	53.61	1.63	34	–0.35	0.04	57.56	1.87	32	–0.10	0.60
Horsefly	53.22	1.31	29	–0.42	0.02	57.00	1.64	28	–0.42	0.02
Late Nadina	48.76	1.19	34	–0.71	<0.01	50.33	1.48	34	–0.75	<0.01
Late Stuart	50.57	1.81	25	–0.66	<0.01	48.94	1.96	25	–0.54	<0.01
Raft	52.44	1.59	30	–0.71	<0.01	57.11	1.48	30	–0.57	<0.01
Stellako	51.31	1.42	40	–0.42	<0.01	53.86	1.37	40	–0.37	0.02

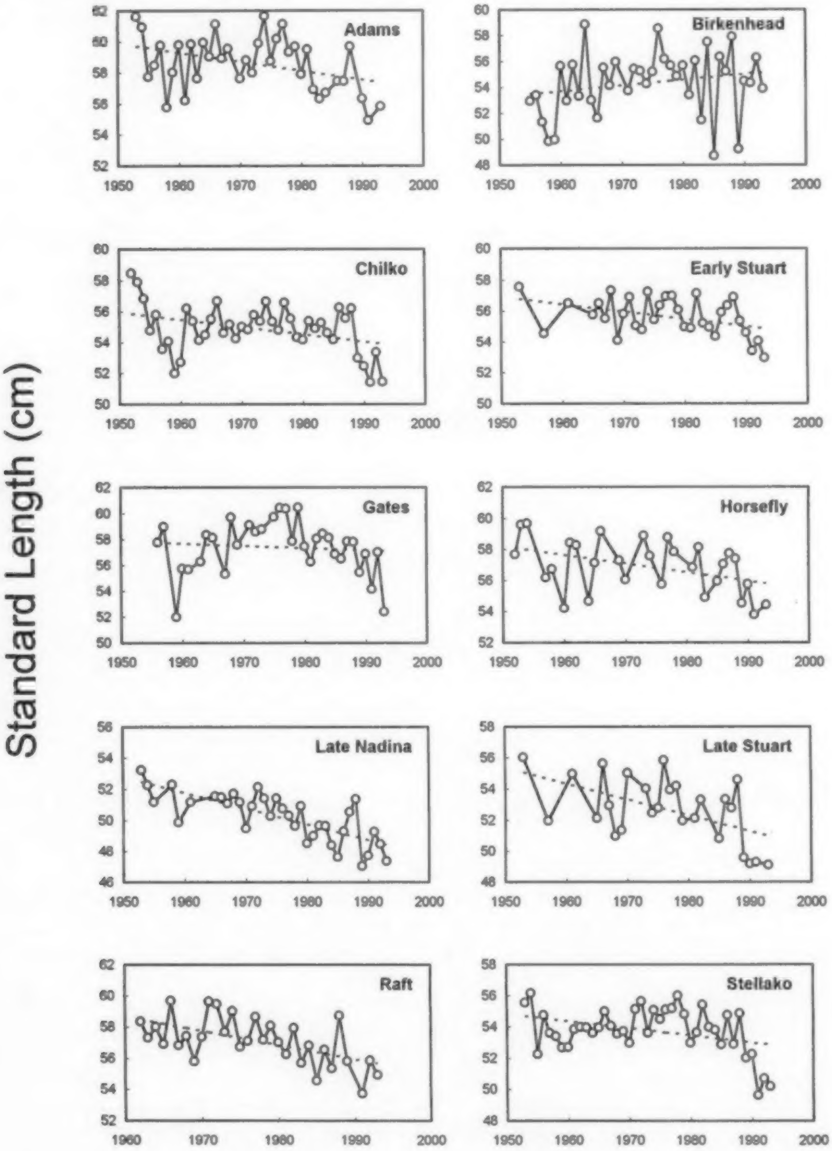
Note: Also shown are the correlation coefficients (and associated probabilities) between standard length and year.

among stocks for females (ANCOVA; $P = 0.17$). This interaction term was then removed from the ANCOVA, revealing a significant effect of year ($P < 0.01$) and stock ($P < 0.01$). In all stocks, female SL declined in a similar fashion over time (Fig. 2; Table 2). Females from Adams, Gates, and Raft stocks tended to have relatively large SL at maturity whereas Late Nadina had a relatively small SL at maturity. The slopes of the regressions of SL on year differed among stocks for males (ANCOVA; $P < 0.01$); the differences were attributable to Birkenhead and Gates stocks where size at maturity showed no time trend (Fig. 3; Table 2). After removing these two stocks from the analysis, the remaining regression slopes did not differ among stocks (ANCOVA; $P = 0.17$). This interaction term was then removed from the ANCOVA, revealing a significant effect of year ($P < 0.01$) and stock ($P < 0.01$). Among the remaining eight stocks, male SL declined similarly over time (Fig. 2; Table 2). Males from Adams and Raft stocks tended to have relatively large SL at maturity whereas the Late Nadina stock had a relatively small SL at maturity. With the exception of males from Birkenhead and Gates stocks, mean length at maturity of Fraser River sockeye salmon declined over time (Figs. 1 and 3; Table 2) and the 1990's produced the smallest Fraser River sockeye salmon out of the previous five decades for both males and females.

Power analyses indicated that MDD among years in stock-specific size at maturity ranged from 0.83 to 1.56 cm for males and from 0.49 to 0.88 cm for females (Table 1). Each of the statistically significant stock- and sex-specific regression relationships between SL and year predicted a decline in size that exceeded the MDD (see Figs. 1 and 3), suggesting that the declines are not the result of low sample size or measurement error in some years. The relatively larger MSE (and MDD; Table 1) of males implies that they varied more in size at maturity than females. This sex-specific difference in size variability has been found in other Pacific salmon species (Beacham and Murray 1985; Healey 1986). Greater within-stock variation in male size at maturity may be due to the presence of alternative mating strategies (e.g., satellite and dominant behaviours) that exist for male Pacific salmon (Hanson and Smith 1967). Size-related variability in female sockeye salmon mating strategies is less well defined.

Mixed-stock commercial catch data have previously been used to examine trends in size at maturity of Canadian salmon (Killick and Clemens 1963; Ricker 1982; Bigler et al. 1996). With the exception of sockeye, Pacific salmon species have demonstrated a decline in size at maturity from the 1950's to the present (Ricker 1995). It is possible that variability in the relative abundance of sockeye salmon stocks could mask a general trend in size at maturity because size at maturity data will reflect the mean size at maturity of the most abundant stocks. This phenomenon is evident in sockeye salmon catch data (Ricker 1995); peaks in size at maturity of Fraser River sockeye caught in commercial fisheries coincide with peaks in the abundance of the Adams River stock which has one of the

Fig. 2. Mean standard lengths of male Fraser River sockeye stocks over a 42-yr period. Missing data points were either not available or excluded due to low sample size ($n < 20$). The broken line represents linear time trend fitted by least squares. Correlation coefficients are reported in Table 2.



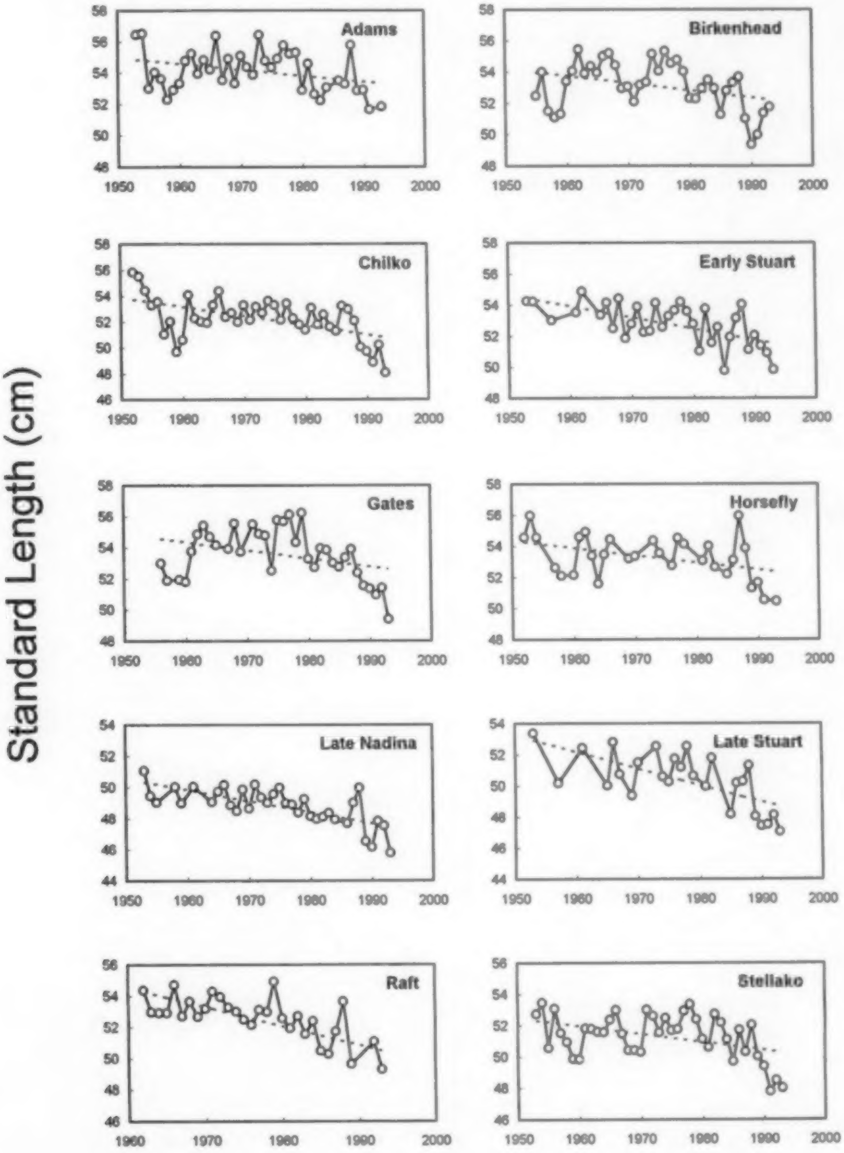
largest sizes at maturity (Table 2). Thus, their large size combined with relatively high abundance may have resulted in a general species trend being obscured in past analyses that used mixed-stock catch data (i.e., Ricker 1995). We conclude that the size at maturity of Fraser River sockeye salmon has exhibited the same general decline over the past four decades that the other major Pacific salmon stocks have displayed.

Size at maturity and SST relationships

Average SST from January to July in the northeast Gulf of Alaska was positively associated with year; SST rose by almost 1°C from the early 1950's to the early 1990's. This temperature increase was first reported by Namias et al. (1988) who identified that a large-scale climate shift, resulting from changes to positions of the main high and low pressure areas, occurred over the northeast Pacific Ocean in 1976. The significant trend that we observed in the SST data indicates a similar punctuated change rather than linear increase (Fig. 4). Since then, average annual SSTs have increased by 1°C in coastal areas and by 0.5°C in high seas areas. (Hourston 1992).

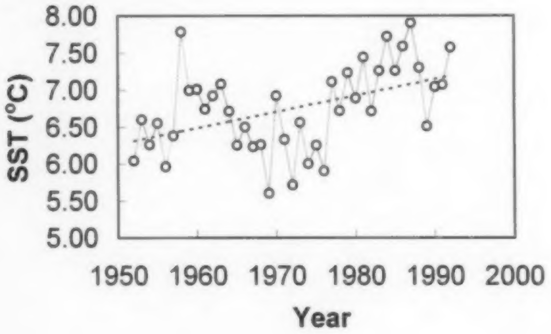
ANCOVA revealed that slopes of the regressions of residual SL on residual SST did not differ among the 10 stocks for

Fig. 3. Mean standard lengths of female Fraser River sockeye stocks over a 42-yr period. Missing data points were either not available or excluded due to low sample size ($n < 20$). The broken line represents linear time trend fitted by least squares. Correlation coefficients are reported in Table 2.



males ($P = 0.07$) or females ($P = 0.18$). These interaction terms were removed and the ANCOVA recomputed. Regression intercepts did not differ among stocks for males ($P = 0.99$) or females ($P = 0.99$). However, slopes differed from zero for both males ($P = 0.01$) and females ($P < 0.01$). The common regression equation between residual SL and residual SST was, for males, residual SL = –0.02 – 0.51 residual SST and, for females, residual SL = –0.01 – 0.32 residual SST. The negative slopes associated with these relationships suggest that the growth of Fraser River sockeye salmon is reduced during relatively warm years of their high-seas residency. Our multistock findings extend the single-stock results of Hinch et al. (1995*a*, 1995*b*) who found a negative association between SST and weight at maturity of the Early Stuart stock of Fraser River sockeye. Ricker (1982), using mixed-stock data collected from several British Columbia river systems before the climate shift of the late 1970's, also found that warmer SST were associated with smaller sockeye salmon. Our results indicate that this relationship was consistently evident at the individual stock level, including the two stocks that did not show a decline in mean size with time, and that the relationship has continued in the two "warm" decades following the climate shift.

Fig. 4. Mean sea surface temperatures (SST) calculated from monthly averages (January–July, inclusive) over the period 1952–1992, inclusive, for a region in the northern Gulf of Alaska (see text).



The slower growth of sockeye salmon may result from increased metabolic demand under warmer ocean conditions which reduces growth potential (Jobling 1994). Hinch et al. (1995*a*) concluded that increased metabolic costs associated with SST increases of the magnitude observed over the past several years could account for observed declines in weight at maturity of the Early Stuart stock. A complimentary hypothesis is that slower growth under warmer ocean conditions may result from reductions in the amount of ocean habitat available, thereby increasing competitive interactions (Welch et al. 1995), because in warm years the southern limit of sockeye salmon distribution is situated farther north than in cool years.

Fraser River sockeye stocks vary in oceanic residence time (Gilhousen 1990) and possibly in oceanic distribution (Blackbourn 1987; Welch and Parsons 1993). The fact that all stocks grew more slowly in warmer years indicates that SST may have powerful, broad-scale influences on sockeye salmon growth. However, size at maturity could be influenced by environmental factors correlated with SST. When the abundance of salmon in the northeast Pacific Ocean is high, size at maturity may be reduced due to density-dependent growth (Peterman 1984, 1985, 1987; Ogura et al. 1991; Helle and Hoffman 1995; Ishida et al. 1995; Bigler et al. 1996). Although the abundance of sockeye salmon in the Gulf of Alaska has doubled over the past, relatively warm 15 yr (Beamish and Bouillon 1993), macrozooplankton biomass has more than doubled during this same time (Brodeur and Ware 1995). Hinch et al. (1995*b*) showed that zooplankton biomass was correlated with size at maturity of Early Stuart sockeye in cool years, but stock abundance also helped explain variation in weight in warm years. The role of SST in mediating density-dependent growth needs to be more fully explored.

Potential impacts of climate warming: sockeye salmon may be in hot water

If we assume that SST is linked with changes in size of sockeye salmon, we can speculate on the potential effects of future climate warming. Global climate models predict that, over the century, the northeast Pacific will experience a 2–4°C increase in SST (Boer et al. 1992). Current trends suggest that the northeast Pacific Ocean has been warming over the past decade; however, it remains uncertain whether the trend is due to global climate warming or a reversal of a regional cooling period that began in 1958 (Zebdi and Collie 1995). In future years, if SST continue to increase and sockeye salmon abundance stays at or near present levels, sockeye salmon may continue to get smaller. Decreases in body weight of mature fish will reduce egg production and the ability to migrate upstream and spawn (Healey 1986). To compensate, sockeye salmon may need to remain at sea for an additional year in order to attain the necessary size and energy reserves to spawn successfully (Peterman 1985; Mangel 1994). However, an older age at maturity would decrease reproductive potential due to an increase in generation time. Increases in average age at maturity associated with increases in SST have been observed in other salmon species, but not sockeye (Ogura et al. 1991; Helle and Hoffman 1995). Hinch et al. (1995*b*) speculated that changes in sea level pressure gradients over the North Pacific associated with global climate warming will cause a decline in upwelling-induced nutrients. Thus, growth could be negatively affected by increases in SST and decreases in prey availability. However, if salmon abundance were to decrease during extended periods of warming, then growth reductions may be less obvious because constraints imposed by density-dependent growth processes could be alleviated.

Acknowledgments

We thank Jim Woodey and Mike Lapointe from the Pacific Salmon Commission for providing the spawning ground data. Ian Jardine provided assistance with the SST data and Fraser River map. Insights from David Welch, Mike Healey, and Mike Lapointe are also appreciated. S.P. Cox was supported a Natural Sciences and Engineering Research Council of Canada strategic grant.

References

Beacham, T.D. and Murray, C.B. 1985. Variation in length and body depth of pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) in southern British Columbia. Can. J. Fish. Aquat. Sci. **42**: 312–319.

Beamish, R.J. and Bouillon, D.R. 1993. Pacific salmon production trends in relation to climate. Can. J. Fish. Aquat. Sci. **50**: 1002–1016.

Bigler, B.S., Welch, D.W., and Helle, J.H. 1996. A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). Can. J. Fish. Aquat. Sci. **53**: 455–465.

Blackbourn, D.J. 1987. Sea surface temperature and the pre-season prediction of return timing in Fraser River sockeye salmon (*Oncorhynchus nerka*). *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 296–306.

Boer, G.J., McFarlane, N.A., and Lazare, M. 1992. Greenhouse gas-induced climate change simulated with the CCC second generation general circulation model. J. Clim. **5**: 1045–1077.

Brodeur, R.D. and Ware, D.M. 1995. Interdecadal variability in distribution and catch rates of epipelagic nekton in the Northeast Pacific Ocean. *In* Climate change and northern fish populations. *Edited by* R.J. Beamish. Can. Spec. Publ. Fish. Aquat. Sci. No. 121. pp. 329–356.

Burgner, R.L. 1991. Life history of sockeye salmon. *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. University of British Columbia Press, Vancouver, B.C. pp. 3–117.

French, R., Bilton, H., Osako, M., and Hartt, A. 1976. Distribution and origin of sockeye salmon in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. No. 34.

Furnell, D.J. and Brett, J.R. 1986. Model of monthly marine growth and natural mortality for Babine Lake sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **43**: 999–1004.

Gable, J. and Cox-Rogers, S. 1993. Stock identification of Fraser River sockeye salmon: methodology and management application. Pac. Salmon Comm. Tech. Rep. No. 5.

Gilhousen, P. 1990. Prespawning mortality of sockeye salmon in the Fraser River system and possible causal factors. Int. Pac. Salmon Fish. Comm. Bull. No. 26.

Groot, C., Bailey, R.E., Margolis, L., and Cooke, K. 1989. Migratory patterns of sockeye salmon (*Oncorhynchus nerka*) smolts in the Strait of Georgia, British Columbia, as determined by analysis of parasite assemblages. Can. J. Zool. **67**: 1670–1678.

Hanson, A.J. and Smith, H.D. 1967. Mate selection in a population of sockeye salmon (*Oncorhynchus nerka*) of mixed age groups. J. Fish. Res. Board Can. **24**: 1955–1977.

Healey, M.C. 1986. Optimum size and age at maturity in Pacific salmon and effects of size-selective fisheries. *In* Salmonid age at maturity. *Edited by* D.J. Meerburg. Can. Spec. Publ. Fish. Aquat. Sci. No. 89. pp. 39–52.

Healey, M.C. 1993. The management of Pacific salmon fisheries in British Columbia. *In* Perspectives on Canadian marine fisheries management. *Edited by* L.S. Parsons and W.H. Lear. Can. Bull. Fish. Aquat. Sci. No. 226. pp. 243–266.

Helle, J.H. and Hoffman, M.S. 1995. Size decline and older age at maturity of two chum salmon (*Oncorhynchus keta*) stocks in western North America. *In* Climate change and northern fish populations. *Edited by* R.J. Beamish.Can. Spec. Publ. Fish. Aquat. Sci. No. 121. pp. 245–260.

Henderson, M.A. and Cass, A.J. 1991. Effect of smolt size on smolt–adult survival for Chilko Lake sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **48**: 988–994.

Hinch, S.G., Healey, M.C., Diewert, R.E., and Henderson, M.A. 1995*a*. Climate change and ocean energetics of Fraser River sockeye (*Oncorhynchus nerka*). *In* Climate change and northern fish populations. *Edited by* R.J. Beamish.Can. Spec. Publ. Fish. Aquat. Sci. No. 121. pp. 439–445.

Hinch, S.G., Healey, M.C., Diewert, R.E., Thomson, K.A., Hourston, R., Henderson, M.A., and Juanes, F. 1995*b*. Potential effects of climate change on marine growth and survival of Fraser River sockeye. Can. J. Fish. Aquat. Sci. **52**: 2651–2659.

Hourston, R.A. 1992. Variability of North Pacific Ocean surface sensible and latent heat fluxes. M.Sc. thesis, University of British Columbia, Vancouver, B.C.

Hsieh, W.W., Lee, W.G., and Mysak, L.A. 1991. Using a numerical model of the Northeast Pacific Ocean to study the interannual variability of the Fraser River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **48**: 623–630.

Ishida, Y., Welch, D.W., and Ogura, M. 1995. Potential influence of North Pacific sea-surface temperatures on increased production of chum salmon (*Oncorhynchus keta*) from Japan. *In* Climate change and northern fish populations. *Edited by* R.J. Beamish. Can. Spec. Publ. Fish. Aquat. Sci. No. 121. pp. 271–275.

Jobling, M. 1994. Fish bioenergetics. Chapman & Hall, London.

Killick, S.R. and Clemens, W.A. 1963. The age, sex ratio and size of Fraser River sockeye salmon, 1915 to 1960. Int. Pac. Salmon Fish. Comm. Bull. No. 14.

Laevastu, T. 1984. The effects of temperature anomalies on the fluctuation of fish stocks. J. Cons. Cons. Int. Explor. Mer, **185**: 214–225.

Mangel, M. 1994. Climate change and salmonid life history variation. Deep-Sea Res. **41**: 75–106.

Namias, J., Yuan, X., and Cayan, D.R. 1988. Persistence of North Pacific sea surface temperature and atmospheric flow patterns. J. Clim. **1**: 682–703.

Nikolsky, G.V. 1963. The ecology of fishes. Academic Press, London.

Ogura, M., Ishida, Y., and Ito, S. 1991. Growth variation of coho salmon *Oncorhynchus kisutch* in the Western North Pacific. Nippon Suisan Gakkaishi, **57**: 1089–1093.

Peterman, R.M. 1984. Density-dependent growth in early ocean life of sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **41**: 1825–1829.

Peterman, R.M. 1985. Patterns of interannual variation in age at maturity of sockeye salmon (*Oncorhynchus nerka*) in Alaska and British Columbia. Can. J. Fish. Aquat. Sci. **42**: 1595–1607.

Peterman, R.M. 1987. Review of the components of recruitment of Pacific salmon. Am. Fish. Soc. Symp. **1**: 417–429.

Ricker, W.E. 1982. Size and age of British Columbia sockeye salmon (*Oncorhynchus nerka*) in relation to environmental factors and the fishery. Can. Tech. Rep.. Fish. Aquat. Sci. No. 1115.

Ricker, W.E. 1995. Trends in the average size of Pacific salmon in Canadian catches. *In* Climate change and northern fish populations. *Edited by* R.J. Beamish.Can. Spec. Publ. Fish. Aquat. Sci. No. 121. pp. 593–602.

SAS Institute. 1988. SAS/STAT user's guide, version 6.03. SAS Institute, Cary, N.C.

Welch, D.W. and Parsons, T.R. 1993. δ^{13}C and δ^{15}N isotope values as indicators of trophic position and competitive overlap for Pacific salmon (*Oncorhynchus* spp.). Fish. Oceanogr. **2**: 11–23.

Welch, D.W., Chigrinsky, A.I., and Ishida, Y. 1995. Upper thermal limits on the oceanic distribution of Pacific salmon (*Oncorhynchus* spp.) in the spring. Can. J. Fish. Aquat. Sci. **52**: 489–503.

Woodruff, S.D., Slutz, R.J., Leane, R.L., and Steurer, P.M. 1987. A comprehensive ocean–atmosphere dataset. Bull. Am. Meterol. Soc. **68**: 1239–1250.

Zar, J.H. 1984. Biostatistical analysis. 2nd ed. Simon & Schuster Co., Englewood Cliffs, N.J.

Zebdi, A. and Collie, J.S. 1995. Effect of climate on herring (*Clupea pallasi*) population dynamics in the Northeast Pacific Ocean. *In* Climate change and northern fish populations. *Edited by* R.J. Beamish.Can. Spec. Publ. Fish. Aquat. Sci. No. 121. pp. 277–290.

Seasonal and spatial variation in the abundance and size distribution of fishes associated with a petroleum platform in the northern Gulf of Mexico[1]

David R. Stanley and Charles A. Wilson

Abstract: Stationary dual-beam hydroacoustics and visual point count surveys were used in tandem to measure the density, target strength, and species composition of fishes associated with a petroleum platform in the northern Gulf of Mexico. Fish densities ranged from 0 to 10.5 fish·m^{-3} during monthly sampling trips from January 1991 to May 1992. Density and target strength were spatially and temporally variable. Target strengths varied significantly with side of the platform, month, and east and north current vectors. Density varied significantly with platform side, month, east current vector, and depth. Density and target strength did not change over 24 h periods or with water temperature. Fish densities were highest adjacent to the platform and decreased significantly beyond 16 m. Approximately 1990 – 28 100 fish were associated with the platform depending on the month. A total of 19 species were observed at the platform, with *Chaetodipterus faber*, *Caranx fusus*, *Seriola dumerili*, *Balistes capriscus*, *Lutjanus campechanus*, and *Archosargus probatocephalus* constituting 97% of observed fishes. Based on our results, we conclude that the fishes associated with a petroleum platform conform with the open nonequilibrium hypothesis proposed for fishes in coral reef habitats.

Résumé : Des relevés fondés sur des méthodes de détection hydroacoustique à double faisceau stationnaire et de dénombrement de points à vue ont été utilisés en tandem pour mesurer la densité, l'intensité de cible et la composition en espèces des poissons vivant au voisinage d'un plate-forme pétrolière située dans le nord du golfe du Mexique. La densité des poissons a varié entre 0 et 10,5 poissons·m^{-3} au cours des visites d'échantillonnage mensuelles effectuées entre janvier 1991 et mai 1992. La densité et l'intensité de cible étaient variables dans le temps et dans l'espace. Les intensités de cible ont varié de manière statistiquement significative avec le côté de la plate-forme, le mois et les vecteurs est et nord du courant. La densité a varié de manière statistiquement significative avec le côté de la plate-forme, le mois, le vecteur est du courant et la profondeur. La densité et l'intensité de cible n'ont pas changé au cours des périodes de 24 h ni avec la température de l'eau. Les densités de poissons étaient les plus élevées tout juste à côté de la plate-forme pour diminuer de manière importante au-delà de 16 m. Environ 1 990 à 28 100 poissons vivaient dans le voisinage de la plate-forme selon le mois. Dix-neuf espèces ont été relevées, 97 % des poissons observés appartenant aux espèces *Chaetodipterus faber*, *Caranx fusus*, *Seriola dumerili*, *Balistes capriscus*, *Lutjanus campechanus* et *Archosargus probatocephalus*. Nos résultats nous ont amenés à conclure que les poissons vivant dans le voisinage d'une plate-forme pétrolière obéissent à l'hypothèse de non-équilibre ouvert proposée pour les poissons fréquentant les habitats des récifs de coraux.
[Traduit par la Rédaction]

Introduction

Since the first petroleum platform was installed in the northern Gulf of Mexico, fishers and scientists have been aware of their associated nekton assemblages. These petroleum platforms act as artificial reefs, providing habitat that potentially increases the growth and survival of individuals, affording shelter for protection from predation and spawning substrate, and acting as a visual attractant for organisms not otherwise dependent on hard bottom (Gallaway et al. 1981; Continental Shelf Associates 1982; Bohnsak and Sutherland 1985; Bohnsak et al. 1991). Currently there are over 4000 petroleum platforms in the northern Gulf of Mexico, providing an additional 12 km^2 of hard substrate to the approximately 2600 km^2 of natural hard bottom. Unquestionably, the addition of these structures has been one the most extensive marine habitat modifications in the world, and while the effect of the discharge of materials and bioaccumulation from offshore structures on the environment is well documented (Boesch and Rabalais 1987; Avanti Inc. 1991), the impact of habitat modification on the marine fisheries in their vicinity has not been measured.

The mechanisms and processes leading to an increased abundance of fishes near artificial reefs, relative to adjacent environments, are poorly understood (Grove and Sonu 1983; Bohnsak 1989) and will remain difficult to document without standardized fisheries-independent sampling methods. This problem is evident in previous research examining abundance and composition of fish assemblages surrounding petroleum

Received May 17, 1995. Accepted October 10, 1996.
J12921

D.R. Stanley[2] and C.A. Wilson. Coastal Fisheries Institute, Center for Coastal, Energy, and Environmental Resources, Louisiana State University, Baton Rouge, LA 70803–7503, U.S.A.

---

[1] LSU-CFI Publication 96-03.

[2] Author to whom all correspondence should be addressed. e-mail: Stanleylsu@aol.com

platforms (Sonnier et al. 1976; Gallaway 1980; Continental Shelf Associates 1982; Gallaway and Lewbel 1982; Putt 1982; Stanley and Wilson 1990, 1991). These studies used a variety of methodologies including visual surveys by scuba divers, remotely operated underwater vehicles (ROVs), and fixed underwater cameras, as well as catch per unit effort studies utilizing fish traps and angling surveys. The majority of the research to date has been short term, often only a "snapshot" of the abundance and composition of fishes associated with platforms at a single point in time. A primary goal of these previous studies was to quantify abundance of fishes, but many problems were encountered (and acknowledged) due to sampling technique including diver avoidance, limited visibility, and the selectivity of traps and angling surveys.

The complex architecture of platforms, excessive water depths, and low visibility commonly associated with these structures have made censusing the associated fish populations exceedingly difficult; hence, few long-term studies have been undertaken. The first study to encompass a relatively long time scale used a fixed array of 8-mm movie cameras to demonstrate that the abundance and species composition of the fishes at a platform varied from July through September (Putt 1982). Stanley and Wilson (1990, 1991) found that changes in recreational and charter boat catch rates depended on season, size of the platform, and water depth. Unfortunately, abundance and species composition estimates of the various methodologies cannot be directly compared due to individual gear biases and lack of standardization.

The spatial heterogeneity of natural and artificial reefs has limited the use of traditional fisheries gears in evaluating associated fish populations, making visual surveys the method of choice for fisheries assessments in these environments (Bortone and Kimmel 1991). However, the presence of scuba divers, and possibly ROVs, can bias density and species composition estimates, and low visibility conditions can cause underestimation of abundance and species composition (Sale and Douglas 1981; Brock 1982; Bohnsak and Bannerot 1986; Stanley and Wilson 1995). As an alternative to visual surveys, Gerlotto et al. (1989) demonstrated that towed hydroacoustics could be used to determine relative densities of fish at a petroleum platform off Cameroon. One drawback with the use of this equipment is the lack of species composition data and biological information.

In response to the complex architecture of petroleum platforms, the poor environmental conditions (i.e., rough seas and poor visibility) common in the northern Gulf of Mexico, and the difficulty of estimating abundance with traditional fisheries and visual survey techniques, a combination of stationary dual-beam hydroacoustics and visual surveys was used to sample the composition of fishes associated with a petroleum platform. Estimates of absolute abundance and size distribution can be measured hydroacoustically, while visual point count surveys provide species identification and qualitative species composition data. Hydroacoustics has an advantage not found in other reef survey techniques in that it can measure the near-field area of influence of the reef to reflect the total area affected by the reef. Hydroacoustics is not affected by the poor visibility and nepheloid layers common in the northern Gulf of Mexico, can sample at night, detects targets to macrozooplankton sizes, and has a greater range than visual methods.

The objectives of this research were to use stationary dual-beam hydroacoustics in conjunction with visual point count surveys over a 15-mo period to (1) measure and compare species composition, biomass, and target strength distribution of fishes associated with a petroleum structure, (2) determine the effect of environmental variables on abundance and target strength distribution of fishes associated with the platform, and (3) define the spatial, near-field influence of the platform on the abundance of fishes.

Materials and methods

Site description

The production petroleum platform, West Cameron 352 (WC 352), operated by Mobil Exploration and Production USA, Inc., is located at 28°59.35′N, 93°30.35′W, approximately 80 km south of Cameron, Louisiana, in 22 m of water. The platform is an eight-leg steel template platform with eight active wells, is approximately 20 m wide and 45 m long at the waterline, and encloses approximately 19 800 m^3 of water. The platform was installed in 1978, and the nearest platform is located 14.5 km away.

Sampling design

Stationary dual-beam hydroacoustic and visual point count surveys were conducted monthly at the platform from January 1991 through May 1992, with the exceptions of February and May 1991 due to inclement weather and equipment failure.

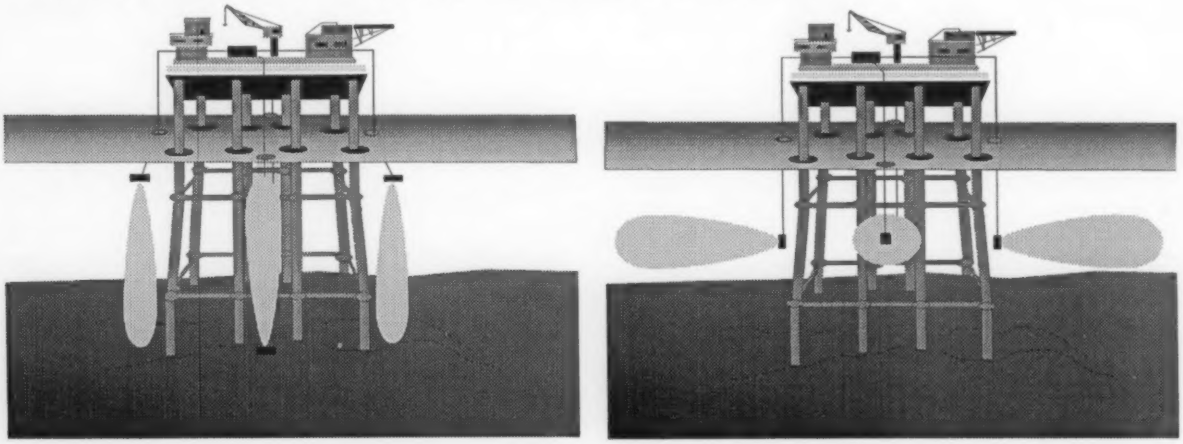
Two arrays of stationary dual-beam hydroacoustic equipment were used. Array 1 was designed to measure the target strength distributions and density of fishes associated with the platform (Fig. 1*a*). It consisted of four vertically oriented transducers: two transducers suspended at the surface facing downwards on the east and north sides of the platform and two transducers placed on the bottom oriented upwards on the west and south sides of the platform. The downward- and upward-facing transducers provided acoustic coverage sufficient to collect acoustic data from 2 to 20 m in the water column in 2-m intervals.

Array 2 was designed to measure the near-field density of fishes associated with the structure (Fig. 1*b*). It consisted of four horizontally aligned transducers, one deployed on each side of the platform at a depth of 11 m. This arrangement allowed for estimates of relative density from 2 to 72 m away from the platform in 7-m intervals.

Horizontal and vertical acoustic sampling was carried out over consecutive 24 h intervals for each month's sampling trip; 2 h of hydroacoustic data were collected encompassing four periods (dawn, noon, dusk, and midnight) over each 24 h interval. Hydroacoustic data were collected sequentially from each of the transducers in 5 min intervals following random selection of the starting transducer for each month. Stationary hydroacoustics allows for the collection of many samples or "snapshots" of density and size distribution over time. The amount of time for an individual sample is dependent on the variance of fish density. Analysis of the variance of density estimates for sample times ranging from 30 s to 15 min in 30-s increments at the study site revealed that the variance of density estimates were not significantly different after a sample duration of 5 min (G. Johnson, Biosonics, Inc., Seattle, WA 98107, personal communication). Therefore, 5 min was used as the duration of an individual sample, and six 5 min samples were collected for each transducer over each time period.

Acoustic data were collected using a Biosonics model 102 echosounder, Biosonics multiplexer equalizer, and Biosonics model 111 thermal chart recorder. Two 120-kHz dual-beam transducers (7°, 18° beam widths) and two 420-kHz dual-beam transducers (7°, 15° beam widths) were used to measure size distribution and density of fishes. Source levels ranged from 216.5 to 219.6 dB re µPa at 1 m varying with transducer. System gains ranged from −178.1 to −184.0 dB re V µPa and from −178.0 to −184.4 dB re V µPa for

Fig. 1. Schematic view of stationary hydroacoustic transducer deployment to measure (*a*) target strength and density of fishes and (*b*) near-field density of fishes associated with the WC 352 petroleum platform in the northern Gulf of Mexico.



20 log R and 40 log R depending on the transducer. From January 1992 to May 1992, a Biosonics model ES2000 scientific echosounder/multiplexer–equalizer was substituted into the suite of equipment replacing the Biosonics model 102 scientific echosounder and multiplexer equalizer. The source levels ranged from 214.0 to 219.6 dB re µPa at 1 m depending on the transducer. The 20 log R system gains ranged from –182.3 to –147.3 dB re V µPa and varied with transducer. The 40 log R system gains ranged from –180.0 to –146.1 dB re V µPa varying with transducer. Sampling rate was $10 \cdot s^{-1}$ for Array 1 and $5 \cdot s^{-1}$ for Array 2, and pulse width was 0.4 ms. Received signals were adjusted for spreading loss by applying a 40 log R time-varied gain, digitized, and recorded on digital audio tape (DAT). Reference voltages (approximately 5 V AC) were recorded on each DAT tape and used to calibrate the acoustic system prior to echo integration and target strength analyses. During data collection, background noise levels were measured at approximately 20 mV at 21 m for Array 1 and 40 mV at 72 m for Array 2. The voltage threshold used in later analyses was 100 mV corresponding to a minimum detectable target strength of –56 dB, or a fish of 2.5 cm total length according to Love (1971).

The hydroacoustic system was calibrated on each research trip with tungsten carbide reference spheres (Foote and MacLennan 1984). Reference targets were suspended approximately 8 m below the transducer and measured target strengths were compared with reference values to provide system calibration.

Digitized hydroacoustic data were processed with a Biosonics model 281 dual-beam processor. Target strengths and an average backscattering cross section (σ) for each depth stratum were estimated using Biosonics TS software (version 2.04), and density estimates were calculated using Biosonics Crunch software with σ for each sample and depth stratum. Fish densities were calculated for 2-m depth vertical intervals for Array 1 and for 7-m horizontal strata for Array 2. Target strength distributions were calculated for 2-m vertical depth intervals for Array 1 for each transducer and sample. Target strength results were not calculated for Array 2 due to the poor relationship and unknown orientation of fishes during horizontal insonification.

During collection of vertical acoustic data, an Interocean S4 current meter was suspended at a depth of approximately 10 m. Current speed (± 0.2 $cm \cdot s^{-1}$), direction (± 0.5°), and temperature (± 0.1°C) were collected every 10 min throughout the sample period.

Visual point count surveys identifying individual fish to species were performed on each sampling expedition (except January and December 1991 due to equipment difficulties) on the east and west sides of the platform using either a Hydrobotics model Orpheus ROV or a Benthos model Mini-Rover ROV or by scuba divers. Visual point count surveys are a standard technique used for assessing abundance and species composition on both natural and artificial reefs (Bohnsak and Bannerot 1986) and have been used in numerous scuba diver, submersible, and ROV surveys (Bohnsak and Bannerot 1986; Bortone et al. 1986, 1989; Shinn and Wicklund 1989). Survey methodology was based on criteria from Bohnsak and Bannerot (1986) and was consistent between ROVs and (or) scuba divers. Visual surveys done with ROVs were recorded on videocassette and the point counts performed later. Species composition data from the visual point counts were then applied to the quantitative abundance estimates based on the hydroacoustics data to estimate fish abundance by species.

Data analysis

Fish density data (number of fish per cubic metre) from echo integration analysis contained a large number of zero values, similar to catch data from traditional fisheries sampling techniques (Pennington 1983, 1985; Shaw et al. 1985; Stanley and Wilson 1991). Therefore, hydroacoustic density data from both Arrays 1 and 2 were transformed by log(density + 1) to approximate the normal distribution.

Two vectors describing current speed and direction to the east–west and north–south were calculated (Pond and Pickard 1983). Currents from the east and north were scaled to positive values; currents from the west and south were scaled to negative values. This scaling provided two vectors that represented current speed and direction for later analyses.

Separate randomized block (RBD) ANOVAs (SAS Institute Inc. 1986) were performed with vertical target strength data and log(density + 1) of vertical density data on depth, time of day (TOD), month, temperature, east and north current vectors, squared east and squared north current vectors, and their interactions, blocking on side of the platform to examine differences due to these variables. Horizontal density data were analyzed with a RBD ANOVA (SAS Institute Inc. 1986) and performed with horizontal log(density + 1) of data on distance from the platform, time of day, month, and their interactions, blocking on side of the platform to examine differences due to the variables. Tukey's studentized range tests (Ott 1982) were used to compare the means of significant variables for vertical and horizontal analyses. Statistical tests were reported as significant at the $\alpha \leq 0.01$ level.

The total abundance estimates at the platform were calculated by determining the near-field area of influence of the platform and then multiplying mean density values (number of fish per cubic metre) for

Table 1. RBD ANOVA (block on platform side) results of target strength (dB) (dependent variable) with platform side, month, TOD, depth, current vectors, temperature, and their interactions at the WC 352 petroleum platform in the northern Gulf of Mexico.

Source	df	SS	MS	*F*	Prob.
Model	470	36369.8446	77.3826	3.56	0.0001
Error	1229	76719.3807	21.7407		
Total	1699	63089.2253		$r^2 = 0.577$	

Source	df	Type III SS	MS	*F*	Pr > *F*
Platform side	3	9060.8021	3020.2674	138.92	0.0001
Month	12	17018.5305	1418.2109	65.13	0.0001
TOD	3	85.5980	28.5327	1.31	0.2688
Depth	8	338.0401	42.2550	1.94	0.0503
East vector	1	425.4606	425.4606	19.57	0.0001
East vector^2	1	358.2685	358.2685	16.48	0.0001
North vector	1	122.1085	122.1085	6.45	0.0179
North vector^2	1	162.0569	162.0569	7.45	0.0064
Temperature	1	58.2670	58.2670	2.68	0.1019
Month·TOD	36	1263.4683	35.0963	1.61	0.0127
Month·depth	96	1355.1263	14.1159	0.65	0.9962
East·north vectors	1	2.7348	2.7348	0.13	0.7229
Month·TOD·depth	306	1630.9832	5.3500	0.25	1.0000

Fig. 2. Monthly density and estimated fish length using dual-beam hydroacoustics at the WC 352 petroleum platform for the study period of January 1991 to May 1992.

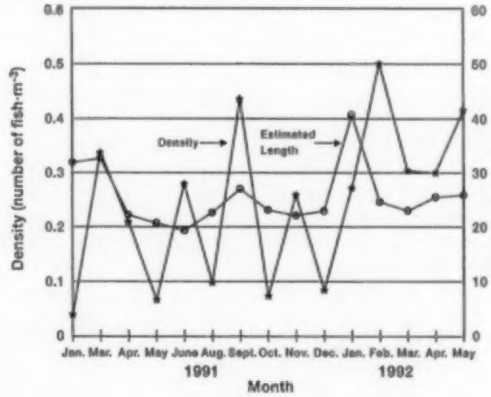
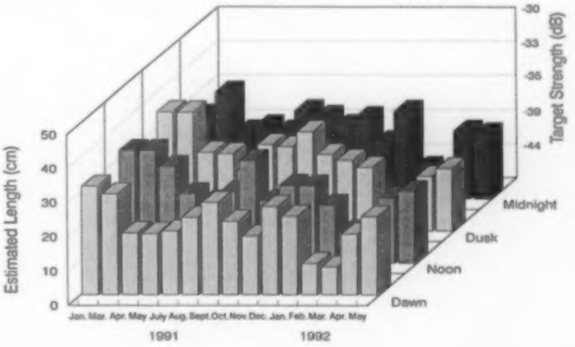


Fig. 3. Mean target strength and estimated length of fishes associated with the WC 352 petroleum platform by month and time of day from January 1991 to May 1992.



each month and platform side by the volume of water on each side of the platform. Fish density in the center of the platform, not measured with acoustics due to interference by structural members, was assumed to be the average of the density estimates of the four sides of the platform. Fish abundance in the center of the platform was calculated by multiplying the estimated fish density of the center by the volume of water in the center of the platform.

Results

Target strength

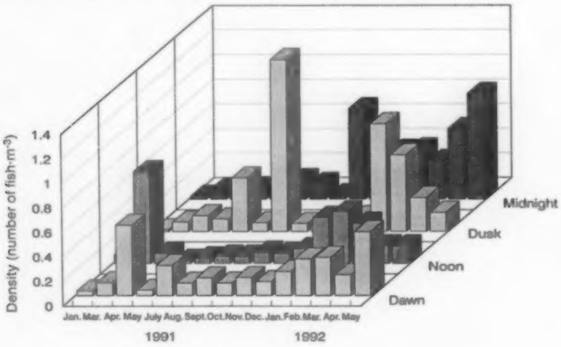
Analysis of the target strength data collected at WC 352 revealed changes in the mean size of fishes over the course of the study. Target strength values ranged from –56 to –24 dB, corresponding to total lengths of 2.5–129.8 cm based on the empirical relationship derived by Love (1971). The RBD ANOVA detected significant differences in mean target strengths between platform sides, months, east current vector, squared east current vector, and squared north current vector variables (Table 1). Two other variables, north current vector and the interaction of month·TOD, were close to being significant (Table 1).

Mean target strength changed significantly between months (Table 1), with largest target strengths occurring in January 1992 (–36.9 dB) and the smallest in April, May, and July 1991 (–41.1, –40.5, and –40.7 dB) (Fig. 2). The general pattern in mean target strengths observed at WC 352 was a maximum in the winter, a decrease through the spring to a minimum in the late spring and summer, and then an increase through the fall (Fig. 2). Diel changes in target strength were not observed (TOD, Table 1). Mean target strength was considered to vary within months over a 24 h period (month·TOD, Table 1). However, a plot of target strengths by month and time of day did not reveal a consistent pattern (Fig. 3), although target

Table 2. RBD ANOVA (block on platform side) results of log fish density (log(number of fish·m^{-3} + 1)) (dependent variable) with platform side, month, TOD, depth, current vectors, temperature, and their interactions at the WC 352 petroleum platform.

Source	df	SS	MS	*F*	Prob.
Model	467	41.141365	0.086431	2.27	0.0001
Error	1350	51.485783	0.038137		
Total	1826	92.627147		$r^2 = 0.444$	
Source	df	Type III SS	MS	*F*	Pr > *F*
Platform side	3	9.176940	3.058980	80.21	0.0001
Month	12	9.928392	0.827366	21.69	0.0001
TOD	3	0.061512	0.020504	0.54	0.6566
Depth	8	0.627121	0.078390	2.06	0.0372
East vector	1	0.275294	0.275294	7.22	0.0073
East vector^2	1	0.000413	0.000413	0.01	0.9172
North vector	1	0.037160	0.037160	0.97	0.3238
North vector^2	1	0.191614	0.191614	5.02	0.252
Temperature	1	0.010699	0.010699	0.28	0.5964
Month·TOD	36	7.703529	0.213987	5.61	0.0001
Month·depth	96	3.920235	0.048358	1.07	0.3068
East·north vectors	1	0.014546	0.014546	0.38	0.5370
Month·TOD·depth	306	6.428990	0.020606	0.54	1.0000

Fig. 4. Mean density of fishes at the WC 352 petroleum platform by month and time of day from January 1991 to May 1992.



strengths were generally larger at low-light periods (dawn, dusk, and midnight) than at high-light periods (noon) (Fig. 3).

Spatially, target strength varied only with side of the platform and not with depth (Table 1). Mean target strengths were significantly larger on the south side (–36.5 dB) of the platform than on all other sides, while mean target strengths were significantly smaller on the north (–40.4 dB) and east (–40.5 dB) sides of the platform.

Target strength varied with current speed and direction based on the significance of both the north and east current vectors and the north and east current vectors squared (Table 1). The relationship between mean target strength and current vectors appeared to be bell-shaped, as midrange target strengths (approximately –40 dB) were found at the highest current vector values, with smaller and larger target strengths more common at low vector values.

Vertical density distribution

Densities of fishes at the WC 352 production platform were highly variable over the study period, ranging from 0 to over 10.5 fish·m^{-3}. Based on a RBD ANOVA, fish density varied significantly with month, platform side, east current vector, and the month·TOD interaction and depth was also close to being significant (Table 2).

Temporal differences in fish density were detected with month and the interaction of month·TOD; however, no general diel trends with fish densities were found (Table 2). Within month, fish densities varied significantly with time of day, although the pattern was not consistent. Generally, densities were lowest at noon and then increased, with maximums occurring at dusk or midnight (Fig. 4). Over the course of the study, monthly fish densities were highest in February 1992 (0.503 fish·m^{-3}) and lowest in January 1991 (0.039 fish·m^{-3}) (Fig. 2). A discernable pattern in the change of fish densities from month to month was not observed; densities varied by up to a factor of 5 between months (Fig. 4).

Spatially, density of fishes varied significantly with side of the platform and water depth (Table 2). Highest fish densities were observed on the north (0.330 fish·m^{-3}) and east (0.373 fish·m^{-3}) sides of the platform, and lower densities were found on the south (0.186 fish·m^{-3}) and west (0.081 fish·m^{-3}) sides. Fish density also varied in the vertical plane and was significantly higher from 4 to 12 m than from 16 to 20 m at the 0.05 level of significance (Fig. 5).

Only the east current vector significantly influenced fish density (Table 2). Highest fish densities were found at lower current speeds, and as current speeds increased, fish densities generally decreased.

Horizontal density distribution

Horizontal density of fishes varied temporally and spatially at the platform. Spatially, horizontal fish density varied with side of the platform and distance from the platform (Table 3). Fish density decreased significantly with distance from the platform. Densities from 2 to 9 m and from 9 to 16 m were significantly higher than those from 16 to 72 m (Fig. 6). Although density varied with side, the pattern of decreasing fish density with distance was consistent for each side of the platform

Table 3. RBD ANOVA (block on platform side) results of log horizontal fish density (log(number of fish·m^{-3} + 1)) (dependent variable) with platform side, month, TOD, distance, and their interactions at the WC 352 petroleum platform.

Source	df	SS	MS	*F*	Prob.
Model	526	7.765838	0.014734	1.80	0.0001
Error	1413	11.604944	0.008213		
Total	1939	19.370782		$r^2 = 0.40$	
Source	df	Type III SS	MS	*F*	Prob.
Platform side	3	0.165177	0.055059	6.70	0.0001
Month	12	0.553437	0.046120	5.62	0.0001
TOD	3	0.014514	0.004839	0.59	0.6222
Distance	11	1.887866	0.171624	20.90	0.0001
Month·TOD	36	0.434518	0.017070	1.47	0.367
Month·distance	108	2.422520	0.022431	2.73	0.0001
Distance·TOD	29	0.124195	0.004283	0.52	0.9835
Month·TOD·distance	324	2.297071	0.007088	0.87	0.9499

Fig. 5. Mean fish density and 95% CI by depth stratum at the WC 352 petroleum platform from January 1991 to May 1992.

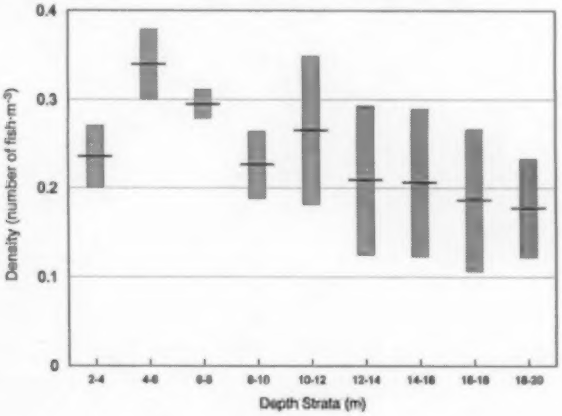
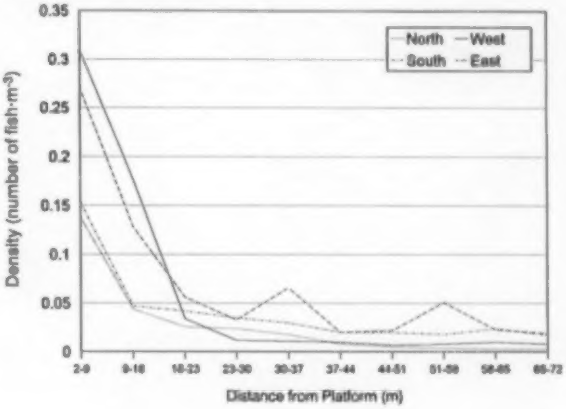


Fig. 6. Mean horizontal density of fish from 2 to 72 m away from the WC 352 petroleum platform for each side of the platform from January 1991 to May 1992.



(Fig. 6). Temporally, horizontal fish density varied significantly between months, but not with time of day (Table 3).

Horizontal fish densities were used to measure the near-field area of influence of the platform. Based on the decrease in fish density with distance from the platform, the near-field area of influence was estimated at 16 m (Table 3; Fig. 6). Beyond 16 m, fish densities dropped off significantly and fish densities were not significantly different from 16 to 72 m (Fig. 6). Because fish density was significantly less in the 9–16 m stratum, relative to the 2–9 m stratum, we calculated a conservative abundance estimate by scaling fish densities in the 9–16 m stratum by 0.510 (the ratio of mean horizontal fish densities from the two strata, i.e., 0.100 fish·m^{-3} ÷ 0.196 fish·m^{-3}).

Total abundance estimates

Total number of fish around the platform was estimated using vertical density estimates averaged for each month and platform side and then extrapolated to 16 m away from the platform for each side of the platform. Vertical fish densities from 9 to 16 m were scaled by 0.510. Fish density in the center of the platform was not directly measured and was estimated by averaging the density estimates of the four sides of the platform. The total number of fish associated with each side of the platform was estimated by multiplying the mean number of fish per cubic metre by the volume of water on each side and in the center of the platform; these numbers were then summed to estimate total number of fish by month associated with the platform (Table 4).

Estimated total number of fish varied with month from a low of 1988 ± 413 in January of 1991 to a high of 28 138 ± 5532 in February 1992 (Table 4). Total abundance estimates were highly variable from month to month (Table 4). The maximum variation of fish abundance by month was approximately 6.6 times, between January and February 1991 (Table 4). Little pattern in abundance estimates was detected with respect to month or season; the only describable pattern was higher densities in 1992 than in 1991 (Table 4). The average number of fish at the platform over the study period was 12 473 ± 3251.

Visual survey results

A total of 19 species were observed over the course of the study; however, only five species, consisting of Atlantic

Table 4. Results of ROV or diver visual point count surveys and estimated number of fish for each species present by month at the WC 352 petroleum platform.

	Percent composition (estimated number)												
	1991								1992				
Species	Mar.	Apr.	May	July	Aug.	Sept.	Oct.	Nov.	Jan.	Feb.	Mar.	Apr.	May
Almaco jack	—	—	—	—	—	—	0.2	0.2	—	—	—	—	0.1
(*Seriola rivoliana*)							(8)	(36)					(21)
Atlantic spadefish	41.5	53.3	35.5	41.6	36.9	36.7	27.9	41.6	18.4	54.9	32.4	12.8	8.6
(*Chaetodipterus faber*)	(6046)	(6046)	(1062)	(5601)	(1922)	(7578)	(1093)	(7479)	(2919)	(14 394)	(5148)	(1859)	(1859)
Bluefish	23.0	0.1	0.5	0.4	—	7.0	20.8	1.9	—	2.6	11.8	23.8	0.1
(*Pomatomus saltatrix*)	(3351)	(12)	(15)	(54)		(1445)	(815)	(342)		(682)	(1875)	(3456)	(21)
Blue runner	2.5	12.1	23.4	15.6	32.7	29.5	19.9	28.7	—	6.9	16.1	21.5	45.3
(*Caranx crysos*)	(364)	(1399)	(700)	(2100)	(1703)	(6091)	(780)	(5160)		(1809)	(2558)	(3122)	(9580)
Black drum	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—
(*Pogonias cromis*)	(29)				(10)								
Cobia	—	—	—	0.1	—	—	—	—	—	—	—	—	—
(*Rachycentron canadum*)				(14)									
Cubbyu	—	—	—	—	—	—	0.2	—	—	—	—	—	—
(*Equetus umbrosus*)							(8)						
Gag	—	—	—	—	—	—	—	0.1	—	—	—	0.1	—
(*Mycteroperca microlepis*)								(18)				(15)	
Gray triggerfish	1.9	1.0	0.5	—	1.4	0.8	0.1	—	0.2	—	—	0.5	0.6
(*Balistes capriscus*)	(277)	(116)	(15)		(73)	(165)	(4)		(32)			(73)	(127)
Greater amberjack	4.4	2.5	1.5	3.4	1.0	0.8	0.7	2.4	4.0	1.8	1.4	5.2	5.7
(*Seriola dumerili*)	(641)	(289)	(45)	(458)	(52)	(165)	(27)	(432)	(635)	(472)	(222)	(755)	(1205)
Jack crevelle	—	—	—	—	—	0.4	—	0.4	0.2	—	—	0.1	0.1
(*Caranx hippos*)						(83)		(72)	(32)			(15)	(21)
King mackerel	—	—	—	—	0.1	—	—	—	—	—	—	—	—
(*Scomberomorus cavalla*)					(5)								
Little tunny	—	—	—	—	1.4	—	1.7	—	—	—	3.5	—	—
(*Euthynnus alletteratus*)					(73)		(67)				(556)		
Lookdown	—	—	—	0.1	—	—	—	0.5	—	—	—	—	0.5
(*Selene vomer*)				(14)				(90)					(106)
Gray snapper	—	—	0.2	0.7	—	—	—	—	—	—	—	0.6	0.7
(*Lutjanus griseus*)			(6)	(94)								(87)	(148)
Red snapper	8.3	10.5	26.9	22.4	19.3	15.1	13.3	19.1	51.7	27.0	1.59	25.5	20.6
(*Lutjanus campechanus*)	(1209)	(1214)	(805)	(3016)	(1005)	(3118)	(521)	(3423)	(8202)	(7078)	(2526)	(3703)	(4356)
Sailors choice	—	—	—	—	0.2	—	2.6	—	—	5.7	9.8	3.4	—
(*Haemulon parra*)					(10)		(102)			(1494)	(1557)	(494)	
Scamp	—	—	0.1	0.1	0.1	0.1	0.2	0.1	—	—	0.2	—	—
(*Mycteroperca phenax*)			(3)	(14)	(5)	(21)	(8)	(18)			(32)		
Sheepshead	18.1	20.4	11.4	15.8	6.6	9.6	12.5	5.1	25.5	2.6	8.8	6.6	18.3
(*Archosargus probatocephalus*)	(2637)	(2359)	(341)	(2127)	(344)	(1982)	(490)	(917)	(4046)	(682)	(1398)	(958)	(3870)
Total	—	—	—	—	—	—	—	—	—	—	—	—	—
	(14 569)	(11 565)	(2992)	(13 464)	(5208)	(20 651)	(3919)	(17 979)	(15 869)	(28 138)	(15 889)	(14 522)	(21 152)

spadefish, blue runner, greater amberjack, red snapper, and sheepshead, were observed on every visual survey (Table 4). Gray triggerfish and bluefish were observed on 9 and 10 of the 13 visual surveys, respectively (Table 4). These seven species made up an average of 97.3% of the fishes surveyed over the study period. There did not appear to be a difference in the species observed between surveys conducted by scuba divers and the ROVs.

Estimated number of fish for each species was calculated by multiplying estimated total abundance by percent composition of that species for each month. Atlantic spadefish, blue runner, and red snapper were the numerically dominant species observed during the study (Table 4). Over the study period, Atlantic spadefish abundance was highly variable. Little pattern in abundance was detected, with the exception of its being the most common fish found (Table 4). Bluefish numbers were highly variable, ranging from a high of 23.8% of fishes observed in April 1992 to <0.5% on numerous occasions (Table 4). Blue runner presence was also variable, with a high of 45.3% in May of 1992 to 0% in January 1992 (Table 4).

Over the study period, blue runner constituted approximately 20% of the fishes, although its abundance appeared to decrease during winter (Table 4). Gray triggerfish made up less than 2% of the fishes found (Table 4). Greater amberjack was detected on every point count survey, although its numbers were low and made up 1–4% of the fishes (Table 4). Red snapper was one of the most common species observed (8.3–51.7%); its abundance was highly variable with respect to time and changed by up to a factor of 4 between months (Table 4). Red snapper abundance appeared to increase from November through February (Table 4). Sheepshead was also observed on every visual survey; it was one of the most common species observed, composing approximately 10% of the fishes found, but no pattern to its abundance was detected (Table 4). Twelve other species of fish were observed at WC 352, individually accounting for less than 1% of the fishes associated with the platform, with the exception of sailors choice. Sailors choice is a small (<20 cm) schooling, demersal grunt (Haemulidae) that may be abundant; however, due to low visibility conditions near the bottom, visual detection of this species was probably inadequate.

Discussion

Temporal and spatial variation was observed in species composition, abundance, and size distribution of fishes associated with a typical petroleum platform in the northern Gulf of Mexico. We found that fish density varied with platform side and depth and that target strength varied with side of the platform, confirming the requirement of comprehensive spatial sampling to describe the assemblages associated with these artificial reefs. The ability to measure changes in density throughout the water column is crucial, as previous researchers were unable to accurately survey nekton in the low-visibility zones of the nephloid layers. We found fish density to be significantly lower in these low-visibility regions, evidence that visual surveys alone could not enumerate these fishes and would underestimate total fish numbers.

There was little or no relationship between current direction and fish density. The effect of current on spatial variation in fish density has been observed by other researchers. Putt (1982) and Continental Shelf Associates (1982) speculated that higher fish densities were found up-current of petroleum platforms, while Chang (1985) concluded that fish were found down-current of artificial reefs. Median current speed and direction over the course of this study was <15 $cm \cdot s^{-1}$ from the east-southeast and the maximum current speed measured was 48 $cm \cdot s^{-1}$. Blaxter (1969) noted that most fish can withstand current speeds 3–4 times their body length for extended periods of time. Therefore, it appears that the current speeds at WC 352 were not strong enough to produce a significant effect on fish behavior causing aggregations up- or down-current of the platform.

Current speed and direction affected target strength at WC 352. Midrange target strengths (approximately –40 dB) were detected at the highest current vector values whereas the smallest target strengths (greater than –45 dB) were associated with low current vector values. The decrease in target strength with increasing current speed suggests that smaller fish were not found at the platform during high current events.

Density and target strength did not vary consistently over shorter periods (e.g., 24 h), unlike observations near other artificial and natural reefs. Past studies have documented off-reef feeding of many species and the subsequent drop in fish densities at night (Hobson 1972, 1975; McFarland et al. 1979; Heffman et al. 1982; Thorne et al. 1989). Based on the potential visual acuity of reef fishes, Munz and McFarland (1973) and Collins and Pettigrew (1988) hypothesized that reef fishes should exhibit diurnal behavior with increased presence at reef sites during the day due to heightened visual acuity. As light levels decrease, visual acuity decreases and fishes should become less attracted to the structure. If fishes at WC 352 exhibited phototaxis, or if off-reef feeding was prevalent at night, then densities should have decreased during the low-light periods. However, densities were generally higher, but not significantly so, at low light levels, perhaps evidence that fishes were attracted to the artificial lights present on the structure, thereby masking any diel variations.

The large monthly variation observed in size distribution and density of fishes at WC 352 is consistent with previous research at natural and artificial reefs in temperate and tropical environments. Fish abundance at reefs is thought to be regulated by physical (density-independent) and biological (density-dependent) factors, deterministic or stochastic effects, and habitat versus recruitment limitation (reviews by Bohnsak et al. 1991; Ebeling and Hixon 1991; Sale 1991). The current hypothesis regarding the abundance of fish at reefs is an open nonequilibrial system that is recruitment limited (Doherty and Williams 1988; Ebeling and Hixon 1991; Sale 1991). This hypothesis suggests that substantial spatial and temporal change occurs in the local reef populations and that this change is primarily due to variable recruitment of fish to reefs. Along with variable recruitment, extreme physical conditions (e.g., turbidity, temperature changes) as well as biological factors such as competition and predation affect assemblages (Talbot et al. 1978; Bohnsak and Talbot 1980; Gascon and Miller 1981; Bohnsak and Sutherland 1985; Doherty and Sale 1985; Shulman and Ogden 1987; Doherty and Williams 1988; Mapstone and Fowler 1988; Jones 1991). Physical factors cause large changes in fish abundances in reef systems (Talbot et al. 1978; Bohnsak and Talbot 1980; Lukens 1981; Bailey-Brock 1989; Relini and Relini 1989), while biological factors reportedly cause a more gradual change in abundance and species composition (Menge and Sutherland 1976; Connell 1980; Bohnsak et al. 1991).

The fish abundance patterns observed at WC 352 appear to fit the open nonequilibrium hypothesis. The density and size distribution of fishes at WC 352 was highly variable from month to month, suggesting that emigration, immigration, and possibly recruitment were driving these changes. Because the variations in target strength and density could vary by up to a factor of 5 between months, it is unlikely that competition and (or) predation caused these large observed fluctuations. The physical factors apparently regulating the large observed changes in abundance were not documented by this study. During sampling periods, temperature had no relationship with density and target strength, and while current speed and direction influenced target strength significantly, only a small effect on density was observed. Stochastic events (e.g., extremes in temperature and dissolved oxygen, storms, strong currents) occurring between sampling trips, and not measured, may have caused the changes. The large fluctuations in fish abundance near artificial reefs in the northern Gulf of Mexico have been attributed to seasonal changes and physical disturbances (e.g., low water temperatures), with lowest abundances in the winter (Gallaway 1980; Lukens 1981; Gallaway and Lewbel 1982; Putt 1982). However, we detected high abundances of fishes in the winter and the differences with past research are probably due to survey techniques. The low abundances previously reported in the winter may be an artifact of the low visibilities known to bias visual survey techniques. Bohnsak and Bannerot (1986) reported that accuracy of visual survey techniques decreased when visibility was less than 3 m, a common condition during the winter months in the northern Gulf of Mexico.

Comparison of results from WC 352 with other petroleum platform studies in the northern Gulf of Mexico revealed similarities; significant differences in density and abundance occurred spatially and temporally. Mean monthly densities at WC 352 were highly variable and ranged from 0.039 ± 0.007 to 0.507 ± 0.117 fish·m^{-3}. Putt (1982) estimated that densities ranged from 0.270 to 0.397 fish·m^{-3} for a petroleum platform off the Texas coast. These numbers are probably an overestimate because densities were calculated over 80 min periods with a fixed camera system, allowing for multiple detection of the same fish. According to visual point count criteria developed by Bohnsak and Bannerot (1986), stationary visual fish count observations should be limited to a 10 min period, with 5 min to document the species present and 5 min to enumerate each species. When observation times greater than 5 min are utilized, repetitive enumeration of the same individuals is common. Continental Shelf Associates (1982) used 3 min point count video surveys from a ROV to enumerate the fish associated with four petroleum platforms in June 1980; densities ranged from 0.002 to 0.027 fish·m^{-3}. While the densities from previous studies are comparable with those estimated at WC 352 using hydroacoustics, the visual techniques utilized are of limited value in low visibility and restricted the authors' conclusions to characterizations of fish populations under high-visibility conditions.

The species composition at WC 352 consisted primarily of Atlantic spadefish, blue runner, greater amberjack, red snapper, and sheepshead. Gray triggerfish was common and large schools of bluefish appeared in the fall and winter. These seven species constituted over 97% of the fishes observed. Some species may have been underrepresented, such as sailors choice, a small grunt that was commonly noted in visual surveys when visibility near the bottom was not affected by nephloid layers. These species were also observed in other petroleum platform studies (Sonnier et al. 1976; Gallaway 1980; Continental Shelf Associates 1982; Gallaway and Lewbel 1982; Putt 1982; Stanley and Wilson 1990). Sonnier et al. (1976) and Stanley and Wilson (1990) noted that over 40 species were associated with platforms in the northern Gulf of Mexico, while we detected only 19 species at WC 352. Disparities in species composition and frequency between this and other platform studies are probably due to geographical and temporal variation and the exclusion of cryptic species.

The species composition at WC 352 helped to explain some of the variation in fish abundance. Blue runner is a semipelagic tropical carangid that appeared to decrease in numbers with decreasing temperature (Stanley and Wilson 1991). Its abundance at WC 352 generally followed this trend and decreased somewhat during winter months. Red snapper abundance at WC 352 was highest in the winter, consistent with past research. During the winter, red snapper congregate at reefs (Moran 1986) and then disperse during the summer to spawn (Thresher 1984). Other fluctuations detected in the fish abundances at WC 352 by month and year are most likely due to physical processes. Substantial monthly variations indicate that many of the fish found at the platform were transient, with little or no fidelity to that particular habitat. The large changes in estimates of total abundance demonstrate that platform assessments can be highly variable and that it may prove difficult to extrapolate results of a single platform to large areas on any time scale. The transient nature of fishes at WC 352 was reinforced by tag and recapture studies conducted in conjunction with this study. Only 6 of 49 tagged greater amberjack and 8 of 140 tagged red snapper were recaptured at WC 352 (Beasley 1993; Render 1995). Since the majority of tagged individuals were not recaptured or observed during the visual surveys, it is assumed that they left the study site, supporting the hydroacoustic results that exhibited a large variance in the number of fish over time.

Total fish abundance estimates at WC 352 were higher than those of other platform studies, with an average of 12 473 fish calculated over the study period. Putt (1982) estimated that a platform with a water depth of 20 m had an average of 1924 fish from July through September. Single point count estimates by Continental Shelf Associates (1982) at four platforms off the Louisiana coast, in water depths from 28 to 31 m, found 283–3955 fish associated with individual platforms. Differences in the estimated fish abundances between the WC 352 study and previous studies may be due to the larger near-field area of influence measured in this study. Earlier researchers did not directly measure the near-field area of influence and assumed it to be 5 m. The near-field area of influence measured at WC 352 was 16 m, comparable with that detected by Gerlotto et al. (1989). They found that relative fish densities were significantly higher within 10 m of a petroleum platform than those measured 50 m away. Another possible explanation for the higher total fish abundance estimates at WC 352 may be size of the platform. Previous research (Grove and Sonu 1983; Rountree 1989; Stanley and Wilson 1990) indicated that fish abundance increased with increasing artificial reef size, and the WC 352 petroleum platform was larger than three of the four platforms compared in other studies. The higher abundance of fishes detected at WC 352 than described during other studies could be attributed to the utilization of dual-beam hydroacoustics which did not influence fish behavior, was not limited by visibility, and could determine the area of influence of the reef.

The coupling of two fisheries-independent techniques, dual-beam hydroacoustics and visual point count surveys, has provided the best estimates of fish assemblages associated with a petroleum platform to date. Abundance and size distributions were determined with dual-beam hydroacoustics, while visual point counts provided species composition data. Hydroacoustics also gave the first quantified measurement of the near-field area of influence surrounding an artificial reef. This effect was estimated to be 16 m on each side of the platform based on continuous density estimates from 2 to 72 m. The assemblage of fishes at WC 352 was highly variable, both temporally and spatially, in support of the open nonequilibrial system hypothesis describing fish abundance at reefs. The variation observed at WC 352 occurred over moderate time scales with no overall diel pattern. The effect of current on fish density was not as pronounced as that noted in earlier research. Overall, the fish assemblage at WC 352 was similar to those observed in past research, with the main differences occurring in higher abundances, a larger near-field area of influence, and a lack of diel variation in abundance and size distribution.

Acknowledgments

The authors thank Mobil Exploration and Producing USA, Inc. (MEPUS) for logistical support and access to the West Cameron 352 petroleum platform. We also thank the staff of WC 352 and "Doc" Brinkley, Curtis Cain, Jerry Hagen, Clyde Jones, Jeff Passmore, and Alan Matheison for their help and patience with our activities. Comments by two anonymous reviewers greatly improved the quality of the manuscript. We would also like to acknowledge the help and friendship of Dr. Jeffery Render with this project. This study is part of a dissertation written by the senior author and was supported by the Louisiana Department of Wildlife and Fisheries, Coastal Fisheries Institute, Louisiana State University, MEPUS, and the Mobil Foundation.

References

Avanti Inc. 1991. Environmental assessment for the regulatory impact analysis of the offshore oil and gas extraction industry proposed effluent guidelines. Vol. 1 — Modeled impacts. U.S. EPA Contract No. 68-C8-0015.

Bailey-Brock, J.H. 1989. Fouling development on an artificial reef in Hawaiin waters. Bull. Mar. Sci. **44**: 580–591.

Beasley, M.L. 1993. Age and growth of greater amberjack (*Seriola dumerili*) from the northern Gulf of Mexico. M.Sc. thesis, Louisiana State University, Baton Rouge, La.

Blaxter, J.H.S. 1969. Swimming speeds of fish. FAO Fish. Rep. **62**: 71–100.

Boesch, D.F., and Rabalais, N.W. 1987. Long-term environmental effects of offshore petroleum development. Elsevier Applied Science, New York.

Bohnsak, J.A. 1989. Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? Bull. Mar. Sci. **44**: 631–645.

Bohnsak, J.A., and Bannerot, S.P. 1986. A stationary visual technique for quantitatively assessing community structure of coral reef fishes. NOAA Tech. Rep. NMFS, **41**: 1–15.

Bohnsak, J.A., and Sutherland, D.L. 1985. Artificial reef research: a review with recommendations for future priorities. Bull. Mar. Sci. **37**: 11–39.

Bohnsak, J.A., and Talbot, F.H. 1980. Species packing by reef fishes on Australian and Carribbean reefs: an experimental approach. Bull. Mar. Sci. **30**: 710–723.

Bohnsak, J.A., Johnson, D.L., and Ambrose, R.F. 1991. Ecology of artificial reef habitats. *In* Artificial habitats for marine and freshwater fisheries. *Edited by* W. Seaman Jr. and L.M. Sprague. Academic Press, New York. pp. 61–108.

Bortone, S.A., and Kimmel, J.J. 1991. Environmental assessments and monitoring of artificial habitats. *In* Artificial habitats for marine and freshwater fisheries. *Edited by* W. Seaman Jr. and L.M. Sprague. Academic Press, New York. pp. 177–236.

Bortone, S.A., Hasting, R.W., and Oglesby, J.L. 1986. Quantification of reef fish assemblages: a comparison of several *in situ* methods. Northeast Gulf Sci. **8**: 1–22.

Bortone, S.A., Kimmel, J.J., and Bundrick, C.M. 1989. A comparison of three methods for visually assessing reef fish communities: time and area compensated. Northeast Gulf Sci. **10**: 85–96.

Brock, R.E. 1982. A critique of the visual census method for assessing coral reef fish populations. Bull. Mar. Sci. **32**: 269–276.

Chang, K. 1985. Review of artificial reefs in Taiwan: emphasizing site selection and effectiveness. Bull. Mar. Sci. **37**: 143–150.

Collins, S.P., and Pettigrew, J.D. 1988. Retinal topography in reef fishes. I. Some species with well developed areae but poorly developed streaks. Brain Behav. Evol. **31**: 282–295.

Connell, J.H. 1980. Diversity and coevolution of competitors, or the ghost of competition past. Oikos, **35**: 131–138.

Continental Shelf Associates. 1982. Study of the effect of oil and gas activities on reef fish populations in Gulf of Mexico OCS area. OCS Rep. MMS 82-10. US DOI, MMS, GOM OCS Region, New Orleans, La.

Doherty, P.J., and Sale, P.F. 1985. Predation on juvenile coral reef fishes: an exclusion experiment. Coral Reefs, **4**: 225–234.

Doherty, P.J., and Williams, D.McB. 1988. The replenishment of coral reef fish populations. Oceanogr. Mar. Biol. Annu. Rev. **26**: 487–551.

Ebeling, A.W., and Hixon, M.A. 1991. Tropical and temperate reef fishes: comparison of community structures. *In* The ecology of fishes on coral reefs. *Edited by* P.F. Sale. Academic Press, New York. pp. 509–563.

Foote, J.J., and MacLennan, D.N. 1984. Comparison of copper and tungsten spheres. J. Acoust. Soc. Am. **75**: 612–616.

Gallaway, B.J. 1980. Pelagic, reef and demersal fishes and macrocrustacean/biofouling communities. Vol. 2. *In* Environmental assessment of Buccaneer gas and oil field in northwestern Gulf of Mexico, 1975–1980. *Edited by* W.B. Jackson and E.F. Wilkens. NOAA Tech. Memo. NMFS-SEFC No. 48.

Gallaway, B.J., and Lewbel, G.S. 1982. The ecology of petroleum platforms in the northwestern Gulf of Mexico: a community profile. USFWS Office Biol. Serv. Wash. D.C. FWS 10BS-82/27. Rep. 82-03.

Gallaway, B.J., Martin, L.R., Howard, R.L., Boland, G.S., and Dennis, G.D. 1981. Effects on artificial reef and demersal fish and macrocrustacean communities. *In* Environmental effects of offshore oil production: the Buccaneer gas and oil field study. *Edited by* B.S. Middleditch. Mar. Sci. Vol. 14. Plenum Press, New York. pp. 237–299.

Gascon, D., and Miller, R.A. 1981. Colonization by nearshore fish on small artificial reefs in Burkley Sound, British Columbia. Can. J. Zool. **59**: 1635–1646.

Gerlotto, F., Bercy, C., and Bordeau, B. 1989. Echo integration survey around offshore oil extraction platforms off Cameroon: observations of the repulsive effect on fish of some artificially emitted sounds. Proc. Inst. Acoust. **19**: 79–88.

Grove, R.S., and Sonu, C.J. 1983. Review of Japanese fishing reef technology. Tech. Rep. 83-RD-137. Southern California Edison Company, Rosemead, Calif.

Heffman, G.S., Meyer, J.L., and McFarland, W.N. 1982. The ontogeny of twilight migration patterns of grunts (Pisces: Haemulidae). An. Behav. **30**: 317–326.

Hobson, E.S. 1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull. U.S. **70**: 715–740.

Hobson, E.S. 1975. Feeding patterns among tropical reef fishes. Am. Sci. **63**: 389–392.

Jones, G.P. 1991. Post-recruitment patterns in the ecology of coral reef fish populations: a multifactorial perspective. *In* The ecology of fishes on coral reefs. *Edited by* P.F. Sale. Academic Press, New York. pp. 294–330.

Love, R.H. 1971. Dorsal aspect target strength of an individual fish. J. Acoust. Soc. Am. **62**: 1397–1403.

Lukens, R.R. 1981. Ichthyofaunal colonization of a new artificial reef in the northern Gulf of Mexico. Gulf Res. Rep. **7**: 41–49.

Mapstone, B.D., and Fowler, A.J. 1988. Recruitment and the structure of assemblages of fish on coral reefs. Trends Ecol. Evol. **3**: 72–77.

McFarland, W.N., Ogden, J.C., and Lythgoe, J.N. 1979. The influence of light in the twilight migrations of grunts. Environ. Biol. Fishes, **4**: 9–22.

Menge, B.A., and Sutherland, J.P. 1976. Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. Am. Nat. **110**: 351–369.

Moran, P.J. 1986. The *Acanthaster* phenomena. Oceanogr. Mar. Biol. Annu. Rev. **24**: 379–480.

Munz, F.W., and McFarland, W.N. 1973. The significance of spectral position in the rhodopsins of tropical marine fishes. Vision Res. **13**: 1829–1874.

Ott, L. 1982. An introduction to statistical methods and data analysis. 2nd ed. Duxbury Press, Boston, Mass.

Pennington, M. 1983. Efficient estimators of abundance for fish and plankton. Biometrics, **39**: 281–286.

Pennington, M. 1985. Estimating the relative abundance of fish from a series of trawl surveys. Biometrics, **41**: 197–202.

Pond, S., and Pickard, G.L. 1983. Introductory dynamical oceanography. 2nd ed. Pergamon Press, New York.

Putt, R.E., Jr. 1982. A quantitative study of fish populations associated with a platform within Buccaneer oil field, northwestern Gulf of Mexico. M.Sc. thesis, Texas A&M University, College Station, Tex.

Relini, G., and Relini, L.O. 1989. Artificial reefs in the Ligurian Sea (Northwest Mediterranean): aims and results. Bull. Mar. Sci. **44**: 743–751.

Render, J.H. 1995. The life history of (age, growth and reproduction) of red snapper (*Lutjanus campechanus*) and its affinity for oil and gas platforms. Ph.D. dissertation, Louisiana State University, Baton Rouge, La.

Rountree, R.A. 1989. Association of fishes with fish aggregation devices: effects of structure size on abundance. Bull. Mar. Sci. **44**: 950–959.

Sale, P.F. 1991. Reef fish communities: open nonequilibrial systems. *In* The ecology of fishes on coral reefs. *Edited by* P.F. Sale. Academic Press, New York. pp. 564–600.

Sale, P.F., and Douglas, W.A. 1981. Precision and accuracy of visual census technique for fish assemblages on coral patch reefs. Environ. Biol. Fishes, **6**: 333–339.

SAS Institute Inc. 1986. SAS user's guide: statistics, version 6 edition. SAS Institute Inc., Cary, N.C.

Shaw, R.F., Cowan, J.H. Jr., and Tillman, T.L. 1985. Distribution and density of *Brevoortia patronus* (Gulf menhaden) eggs and larvae in the continental shelf waters off western Louisiana. Bull. Mar. Sci. **36**: 96–103.

Shinn, E.A., and Wicklund, R.I. 1989. Artificial reef observations from a manned submersible off southeast Florida. Bull. Mar. Sci. **44**: 1051–1057.

Shulman, M.J., and Ogden, J.C. 1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. Mar. Ecol. Prog. Ser. **39**: 233–242.

Sonnier, F., Teerling, J., and Hoese, H.D. 1976. Observation on the offshore reef and platform fish fauna of Louisiana. Copeia, **1976**: 105–111.

Stanley, D.R., and Wilson, C.A. 1990. A fishery dependent based study of fish species composition and associated catch rates around petroleum platforms off Louisiana. Fish. Bull. U.S. **88**: 719–730.

Stanley, D.R., and Wilson, C.A. 1991. Factors affecting the abundance of selected fishes near petroleum platforms in the northern Gulf of Mexico. Fish. Bull. U.S. **89**: 149–159.

Stanley, D.R., and Wilson, C.A. 1995. Detection of the effect of scuba divers on fish density and target strength utilizing dual-beam hydroacoustics. Trans. Am. Fish. Soc. **124**: 946–949.

Talbot, F.H., Russell, B.C., and Anderson, G.R.U. 1978. Coral reef fish communities: unstable high diversity systems? Ecol. Monogr. **48**: 425–440.

Thorne, R.E., Hedgepeth, J.B., and Campos, J.A. 1989. The use of stationary hydroacoustic transducers to study diel and tidal influences of fish behavior. Bull. Mar. Sci. **44**: 1058–1064.

Thresher, R.E. 1984. Reproduction in reef fishes. TFH Publications, Neptune City, N.J.

Fertilization of an oligotrophic lake with a deep chlorophyll maximum: predicting the effect on primary productivity

Howard P. Gross, Wayne A. Wurtsbaugh, Chris Luecke, and Phaedra Budy

Abstract: We investigated how epilimnetic fertilization would affect chlorophyll levels and light penetration of oligotrophic sockeye salmon (*Oncorhynchus nerka*) lakes and how the resulting self-shading would affect primary production of the prominent deep chlorophyll maxima (DCM) of the lakes. Epilimnetic nutrient additions to large mesocosms (330 m^3) in Redfish Lake, Idaho, increased levels of primary productivity and chlorophyll *a* but decreased Secchi depths and light available in the metalimnion and hypolimnion. Redfish Lake and other Sawtooth Valley (Idaho) lakes had DCM in which the mean chlorophyll *a* peaks were 240–1000% of mean epilimnetic chlorophyll *a* concentrations. The DCM existed at low light levels and accounted for 36–72% of the lakes' primary production. Simulations using photosynthesis–irradiance (*P–I*) curves demonstrated that fertilization would increase predicted water column primary production by 75–101%. Most of this increase occurred in the epilimnion, with only a slight decrease occurring in the DCM as the result of increased shading.

Résumé : Nous avons cherché à déterminer comment la fertilisation épilimnétique pouvait influer sur les concentrations de chlorophylle et la pénétration de la lumière dans les lacs oligotrophes fréquentés par le saumon sockeye (*Oncorhynchus nerka*) et comment l'ombre autogénérée qui en résulte influe sur la production primaire des maximums de chlorophylle dans la couche profonde (MCP) dominants dans ces lacs. Des ajouts d'éléments nutritifs dans l'épilimnion dans de grands mésocosmes (330 m^3) du lac Redfish en Idaho ont augmenté le degré de production primaire et la concentration de chlorophylle *a*, mais ont diminué la profondeur de transparence au disque de Secchi et la lumière disponible dans le métalimnion et l'hypolimnion. Le lac Redfish et d'autres lacs de la vallée Sawtooth, en Idaho, présentaient des MCP dans lesquels les maximums de la concentration moyenne de la chlorophylle *a* équivalaient à 240–1000 % de la concentration épilimnétique moyenne de chlorophylle *a*. Les MCP existaient à des faibles degrés de luminosité et expliquaient 36–72 % de la productivité primaire des lacs. Des simulations avec des courbes de photosynthèse–irradiation (*P–I*) ont montré que la fertilisation augmenterait la production primaire prévue dans la colonne d'eau de 75 à 101 %. La plus grande partie de cette augmentation est survenue dans l'épilimnion et seule une légère diminution des MCP a été observée à la suite de l'augmentation de l'ombre.
[Traduit par la Rédaction]

Introduction

Managers have used lake fertilization to increase the productivity of sockeye salmon (*Oncorhynchus nerka*) rearing lakes in North America, primarily for commercial purposes (Stockner 1987; Kyle et al. 1988). This approach attempts to enhance trophic transfer throughout the limnetic food chain: increases in a lake's nutrient load cause increases in the productivity of the phytoplankton community, which leads to increases in zooplankton and, ultimately, sockeye production.

We evaluated lake fertilization as a tool to help prevent the extinction of the endangered Snake River sockeye salmon (Budy et al. 1994; Gross et al. 1994; Gross 1995; Luecke et al. 1996). Owing to a drastic decline (>99%) in the numbers of anadromous sockeye salmon in the Sawtooth Valley lakes, central Idaho, U.S.A., resource managers began a hatchery broodstock program to propagate more sockeye salmon than would overwise survive in the lakes (Bevan et al. 1994). As presmolts from this broodstock program are released into the Sawtooth Valley lakes, managers may use lake fertilization to increase the fish's growth and survival rates.

The Sawtooth Valley lakes have deep chlorophyll maxima (DCM) (Budy et al. 1995) that may be affected by lake fertilization. Chlorophyll *a* concentrations in these lakes can be up to 10 times greater in the metalimnia and hypolimnia than in the epilimnia (Steinhart et al. 1994).

DCM in lakes and oceans have varying characteristics that suggest multiple processes contributing to their formation and maintenance (Steele 1964; Anderson 1969; Hobson and Lorenzen 1972). DCM occur in or below the thermocline where light, temperature, and turbulence are low, but nutrients are relatively rich (Moll and Stoermer 1982). Some investigators (e.g., Shortreed and Stockner 1990) maintain that most of the DCM is controlled by differential sinking rates of algal cells generated in the epilimnion, while others (e.g., Fee 1976) conclude that the DCM is generated in situ by substantial levels of primary production. Investigators must exercise caution when assigning ecological significance to the DCM because phytoplankton will often increase pigment production under the low-light conditions of deeper waters (Steele 1964; Hobson and Lorenzen 1972; Kiefer et al. 1976).

Received February 23, 1996. Accepted October 10, 1996.
J13319

H.P. Gross,[1] W.A. Wurtsbaugh, C. Luecke, and P. Budy. Department of Fisheries and Wildlife, Utah State University, Logan, UT 84322-5210, U.S.A.

[1] Present address: SWCA Environmental Consultants, 56 West 400 South, Suite 201, Salt Lake City, UT 84101, U.S.A.
e-mail: hgross96@aol.com

Table 1. Physical and morphometric characteristics of the Sawtooth Valley lakes.

Lake	Surface area (km^2)	Mean depth (m)	Max. Depth (m)	Drainage area (km^2)	Mean summer Secchi depth, 1993 (m)
Redfish	6.15	44	91	108.1	11.9
Alturas	3.38	32	53	75.7	10.4
Pettit	1.62	28	52	27.4	13.2
Stanley	0.81	13	26	39.4	7.3
Yellow Belly	0.73	14	26	30.4	9.2

In some sockeye salmon rearing lakes, juvenile sockeye may primarily reside at metalimnetic depths during part of the growing season owing to temperature limitations (Foerster 1968), consuming a large portion of the metalimnetic zooplankton standing stock (LeBrausser et al. 1978; Shortreed and Stockner 1990). This reduction in metalimnetic zooplankton and corresponding reduction in grazing rate on phytoplankton may also contribute to the maintenance of the DCM.

The DCM in the Sawtooth Valley lakes are located at depths where the light levels are near or below 1% of surface light. Although this light level is nominally given as the bottom of the photic zone, substantial primary production has been measured at lower light levels (Anderson 1969). Increases in phytoplankton, which would result from lake fertilization, should decrease light available in the DCM and lead to a compression of the photic zone (Goldman 1988). Thus, we were interested in the effect this shading could have on the phytoplankton assemblage in the DCM and resultant effects on water column primary production.

Here we describe the DCMs relative contribution to overall lake primary production. We also investigate the possibility of the DCM being an artifact of increases in pigment production under low-light conditions. Finally, we determine the effect of epilimnetic nutrient additions on primary production in the epilimnion and in the DCM. To accomplish these goals, we implemented a lake sampling program, conducted fertilization experiments in large-scale mesocosms, and constructed a primary productivity prediction model. Our work concentrated on one of the Sawtooth Valley lakes, Redfish Lake, because it is the focus of the sockeye salmon recovery program. Data from other Sawtooth Valley lakes are presented for emphasis of certain findings.

Study area

The five study lakes are located in the Sawtooth National Recreation Area in south-central Idaho (44°N, 115°W) at elevations between 1985 and 2157 m (Table 1). The lakes drain the east sides of the pristine, granitic Sawtooth and Smoky Mountains. These deep, steep-sided lakes were formed behind large moraines deposited by glaciers during the Pleistocene.

Nutrient levels in the lakes are low: mean summer total nitrogen (TN) and total phosphorus (TP) concentrations in their epilimnia were 65–95 and 6.5–8.6 µg/L, respectively. Correspondingly, water clarity is high, with Secchi depths ranging up to 19 m (Steinhart et al. 1994). Phytoplankton growth in Redfish Lake is limited primarily by nitrogen and secondarily by phosphorus, both in the epilimnion and in the DCM (Gross 1995). Macrophyte abundance is low. The lakes and their watersheds are highly prized for their recreational and aesthetic values.

Redfish Lake has a very low zooplankton biomass, dominated by *Bosmina longirostris* and *Holopedium gibberum*, with small contributions from *Daphnia rosea*, *Polyphemus pediculus*, *Epischura nevadensis*, and at least two species of cyclopoid copepods (Budy et al. 1995). The fish community includes sockeye and kokanee salmon (both *O. nerka*), bull trout (*Salvelinus confluentus*), northern squawfish (*Ptychocheilus oregonensis*), and rainbow trout (*Oncorhynchus mykiss*) (Beauchamp et al. 1993).

Methods

Lake sampling

Sampling of Sawtooth Valley lakes in 1993 began in March when all of the lakes were sampled through a hole sawed through 50–70 cm of ice. Redfish, Alturas, Pettit, and Stanley lakes were sampled biweekly from mid-May (ice-out) until the beginning of October, and then again in November. Yellow Belly Lake was sampled in March and monthly from June through September.

A Hydrolab H2O® multiparameter water-quality data transmitter was used to take vertical profiles of temperature. Vertical profiles of light extinction were measured using a LI-COR Model LI-1000 datalogger, a deck cell, and an underwater spherical sensor that measured photosynthetic active radiation (PAR; 400–700 nm). Measurements were taken at 2-m intervals until 36 m or to the bottom of the shallower lakes. The light extinction coefficient (Wetzel 1983) was then calculated and used to compute the depth where 1% of surface light remained. Water transparency measurements were made with a 25 cm diameter Secchi disk.

In most of the lakes, chlorophyll samples were collected biweekly from the epilimnion with a tube sampler at three stations. These stations were separated by 200–500 m near the deepest part of each lake. At the central index station additional samples were taken at the 1% light level. At monthly intervals, samples from 5 to 13 other depths were collected at the index station. For chlorophyll analysis, two 50-mL aliquots per sample were filtered through 0.45-µm cellulose acetate membrane filters. (Earlier size-fractionation analyses using Nucleopore filters demonstrated that 0.45-µm filters retained 83–97% of the chlorophyll that was retained by 0.1-µm filters (Budy et al. 1995).) Filters were placed into 6 mL of 100% methanol in the dark for 24–48 h to extract chlorophyll *a*. The extracts were then analyzed before and after acidification (Holm-Hansen and Riemann 1978) using a Turner model 111 fluorometer. Corrections were made for phaeopigments. The fluorometer was calibrated using commercial chlorophyll *a* standards that were verified spectrophotometrically.

Phytoplankton samples were collected monthly from the epilimnion and 1% light level and preserved using Lugol's iodine solution. Additional epilimnetic samples were collected at biweekly intervals from some lakes. A 50- or 100-mL aliquot from each sample was filtered through a 0.45-µm mixed-ester filter (Millipore® HAWP), cleared, and permanently mounted according to the method of Crumpton (1987). Cells were counted in a minimum of 10 fields per slide at 400×; the dimensions of a minimum of 10 individuals in each taxon were measured to calculate biovolume (Wetzel and Likens 1991). Phytoplankton were taxonomically classified as follows: Cyanobacteria (blue-green algae), Chlorophyta (green algae), Chrysophyta (primarily *Dinobryon* sp.), Bacillariophyta (diatoms), and Dinophyta (primarily *Peridinium* sp.).

In situ primary production rates (PPR) of phytoplankton were measured with the ^{14}C-technique (Wetzel and Likens 1991). Measurements were made on three dates in Redfish and Pettit lakes, and once in Stanley and Alturas lakes. Water from each of eight or nine depths was placed into three 25-mL glass scintillation vials, taking care not to expose the plankton to direct sunlight. Each vial was inoculated with 80 µL of 25 µCi/mL of $^{14}CHO_3$–. To measure non-photosynthetic ^{14}C uptake, we inoculated one vial from each depth with 150 µL of a saturated solution of Diuron (dichlorophenyldimethylurea; DCMU), a photosynthetic inhibitor. The vials were resuspended in the water column in clear acrylic plastic tubes hung from an incubation line. Incubations were normally conducted from 10:00 to 14:00 (Mountain Standard Time). After the incubation, the vials were kept in the dark and within 2 h the entire contents of each vial were filtered through 0.45-µm cellulose nitrate filters and rinsed with 0.01 M HCl. They were then air-dried and subsequently counted by liquid scintillation spectrometry using Readysafe® cocktail. Production rates were calculated by subtracting carbon uptake in the DCMU treatments from the light treatments. Dissolved inorganic carbon was estimated from pH and temperature, and alkalinity measurements were determined with the Gran procedure (Wetzel and Likens 1991). Productivity in the water column was partitioned into that occurring in the epilimnion and in the lower strata. Because the lakes were not clearly stratified for much of the summer, we used a nominal depth stratum of 0–7.5 m for calculating the production that occurred in the epilimnion.

Limnocorral experiment

Nutrient addition experiments took place in Redfish Lake in six cylindrical mesocosms (limnocorrals, designed by Aquatic Research Instruments, Seattle, Wash.) over an 11-week period. The 330-m³ limnocorrals were 5 m in diameter and approximately 17 m deep with open tops floated above the lake surface. They were constructed with weighted curtains of impermeable, fiber-reinforced polyethylene. The limnocorrals were unfurled slowly (12 h) through the water column with the bottoms open; thus, the initial conditions were similar to those in the lake. Once filled, SCUBA divers tied the bottoms closed. Each limnocorral was randomly assigned one of three nutrient treatments ($n = 2$):

(1) controls, which received no nutrient additions (CNTL),
(2) low levels of nitrogen (N) and phosphorus (P) additions (LOW), and
(3) high levels of N and P additions (HIGH).

At the start of the experiment, on 29 June, mean total P (TP) and total N (TN) concentrations in the limnocorrals were 5.6 µg/L (range 5.1–5.9 µg/L) and 67 µg/L (range 63–76 µg/L), respectively. In the LOW nutrient treatment we increased P by 75% and N by 125% over the 11-week experiment (i.e., 4.2 µg P/L and 84 µg N/L were added). In the HIGH nutrient treatment P and N concentrations were increased by 150 and 250%, respectively (8.4 µg P/L and 168 µg N/L). Nutrients were added in the form of $(NH_4)_2HPO_4$ and NH_4NO_3, at a 20:1 mass TN:TP ratio. The high TN:TP ratio was used to reduce the likelihood of stimulating nitrogen-fixing cyanobacteria (Schindler 1977; Stockner and Shortreed 1988). Weekly, nutrient solutions were stirred into each limnocorral at the surface. To promote rapid initial growth of the plankton community, 40% of the nutrients were added during the first week of the experiment; the remaining 60% were added in equal parts over the following 10 weeks.

Because the experiment was also designed to determine whether zooplankton and fish growth could be enhanced by nutrient additions, we added 25 native young-of-the-year kokanee in lieu of endangered sockeye salmon to each of the limnocorrals, for a stocking density of 1.3 fish/m². The results of the nutrient additions on zooplankton and fish growth are reported in Budy et al. (1994).

We monitored chlorophyll *a*, primary production, and light in each limnocorral. Monitoring was conducted 7 days after a nutrient addition and immediately before the subsequent addition. Samples were collected weekly for chlorophyll *a* analysis from the epilimnion (0 to 4, 5, or 6 m, deepening during the summer) with a depth-integrating vinyl tube. Biweekly, we collected additional chlorophyll samples from the metalimnion and near the bottom of the limnocorral with a 4-L Van Dorn bottle. At 1, 4, and 8 weeks of the experiment, ^{14}C primary productivity measurements were made at five depths using the methods described above. Additional depths were sampled for chlorophyll *a* analysis concurrent with the primary productivity measurements. Water transparency measurements were made weekly with a 25-cm black and white Secchi disk. Vertical profiles of light intensity were measured every 2–4 weeks as described above, except that measurements were taken at 1-m intervals from depths of 0 to 17 m.

Table 2. Chlorophyll *a* concentrations (Chl. *a*, µg/L) in the epilimnion and at the deep chlorophyll maximum (DCM) peaks in the Sawtooth Valley lakes during June–October 1993.

Lake	Mean epilimnetic Chl. *a*	Mean DCM peak	DCM peak range	% increase in mean DCM peak over mean epilimnetic Chl. *a*
Redfish	0.6	3.1	2.2–4.8	420
Alturas	0.8	2.7	2.0–3.4	240
Pettit	0.5	3.3	2.0–4.4	560
Stanley	1.1	2.4	1.6–4.5	120
Yellow Belly	0.6	6.6	2.6–8.2	1000

Primary production prediction modelling

Because the DCM peaked below 20 m in Redfish Lake, the 17-m bottom boundary of the limnocorrals prevented us from determining, in situ, what effects shading caused by epilimnetic fertilization would have on the DCM. Therefore, we used a modelling approach to (*i*) simulate the decline in PPR in the DCM that might result from shading associated with fertilization; (*ii*) compare the reduction in PPR in the DCM with the enhancement of PPR in the epilimnion; and (*iii*) compare total simulated water column PPR under fertilized and unfertilized conditions.

To predict PPR depth profiles for Redfish Lake under the altered light and chlorophyll conditions expected with fertilization, we used photosynthesis–irradiance curves (*P–I* curves; Reynolds 1984). These curves relate irradiance (I) to photosynthetic rate (P^B, normalized to chlorophyll *a* biomass). They were produced using PPR, chlorophyll *a*, and irradiance data collected during the lake sampling and ^{14}C measurements. The average depth-specific irradiance for the duration of each ^{14}C measurement was used. Data from six of the eight PPR profiles measured in the Sawtooth Valley lakes were used; two profiles were excluded (Redfish Lake, 4 July 1993, and Pettit Lake, 7 August 1993) owing to incomplete data.

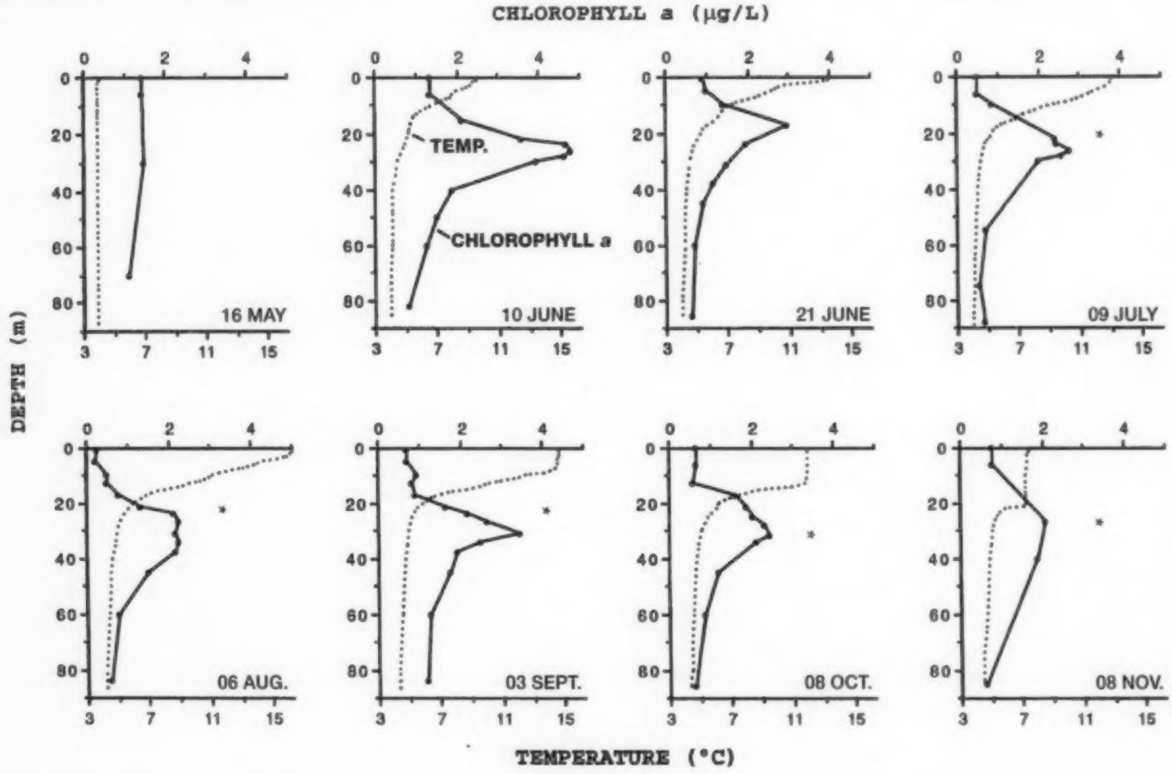
Parameters of the *P–I* curve, such as the initial slope of the light-limited portion of the curve (α) and the maximum photosynthetic rate (P^B_m), are affected by factors such as temperature, nutrient conditions, and the species comprising the algal community. In addition, photoinhibition (characterized by β) can occur above a threshold light intensity (I_T); β and I_T also can vary with environmental conditions.

To partially account for the variations of the *P–I* curves' parameters with depth, we used two *P–I* curves. We separated our samples into two groups using the bottom of the thermocline, which provides an impediment to mixing, as the delineator (Platt et al. 1982). The *P–I* curve for samples from below the thermocline was fit using eq. 8 from Jassby and Platt (1976), which is based on two parameters, α and P^B_m:

$$(1) \qquad P^B_z = P^B_m \cdot \tanh(\alpha I_z / P^B_m)$$

where P^B_z is the P^B at depth z and I_z is the light intensity at depth z. (PPR profile predictions were also attempted using two different linear *P–I* models for below the thermocline; the results varied by 0.3–4.1% from those derived using the Jassby and Platt (1976) model.) The samples above the bottom of the thermocline were fit using the method of Neale and Richerson (1987), which includes β and I_T, thus accounting for photoinhibition, which was frequently observed in the shallower depths of the Sawtooth Valley lakes:

Fig. 1. Chlorophyll a concentration (µg/L) (solid line) and temperature (°C) (dotted line) profiles for Redfish Lake, 1993. When present, an asterisk represents the 1% light level.



(2) $P_z^B = P_m^B \tanh(\alpha I_z/P_m^B)*e^{-\beta*c}$

where $c = 0$ if $I_z \leq I_T$ and $c = I_z - I_T$ if $I_z > I_T$.

The parameters for the P–I curves were derived using the primary productivity, chlorophyll, and light data from the lake sampling program and Gauss–Newton nonlinear regressions (NLIN procedure; SAS Institute Inc. 1988).

The P–I curves were then used to predict and compare vertical primary productivity profiles under fertilized and unfertilized conditions. Predictions for unfertilized conditions were made using light and chlorophyll levels observed in the lake. Predictions for PPR profiles under fertilized conditions were based on the following alterations of observed chlorophyll and light levels:

(1) The chlorophyll levels in the top 17 m (depths of 0.5, 5, 10, 13, and 17 m) were boosted over values observed in the lake by the increases we saw in the limnocorrals owing to the LOW levels of nutrient additions. The LOW level was chosen because it most closely resembled levels that would be used for a whole-lake fertilization.

(2) Light intensity at each depth was computed using the following equation, which modifies the ambient light level in the lake to include the shading caused by increases in phytoplankton resulting from the nutrient treatments:

(3) $I_z = I_0 \cdot (e^{-LE_{trt} \cdot z_1}) \cdot (e^{-LE_{cntl} \cdot z_1})^{-1} \cdot (e^{-LE_{lake} \cdot z_2})$

where I_z is the light intensity in water at depth z, I_0 is the light intensity in water at depth 0, LE_{trt} is the mean light extinction coefficient in nutrient treatments (e.g., LE_{low} or LE_{high}), LE_{cntl} is the mean light extinction coefficient in CNTL treatments, and LE_{lake} is the light extinction coefficient in the lake. For z = 0–17 m, $z = z_1 = z_2$. For $z >$ 17 m, $z = z_2$, $z_1 = 17$ m. LE_{trt} and LE_{cntl} were selected to represent the levels of shading observed in the limnocorrals (the greater the difference between LE_{trt} and LE_{cntl}, the greater the level of shading). Thus, by using recorded light extinction coefficients representing the upper, intermediate, and lower levels of shading observed in the limnocorrals, we tested the sensitivity of the shading parameter.

This approach assumes that all of the added nutrients remained in the top 17 m of the water column, stimulating the phytoplankton there. In the lake, some of these nutrients would be transported to the DCM through sedimentation and other mixing processes, possibly stimulating phytoplankton growth there (depending on whether this layer is light and (or) nutrient limited).

Results

Lake sampling

Deep chlorophyll maxima (DCM) existed in the Sawtooth Valley lakes during the ice-free stratified season (Fig. 1). In mid-May, Redfish Lake was isothermal and chlorophyll levels were nearly homogenous from 0 to 70 m, indicating that the lake mixed to the bottom in 1993. By 10 June, a DCM was observable, and it persisted through November, when the thermocline began to erode with the approach of fall overturn. The DCM peak was located below the thermocline, near and frequently below the 1% light level (Fig. 1). Similar DCM patterns occurred in the other Sawtooth Valley lakes (Budy et al. 1995; Gross 1995). The peak levels of chlorophyll a in the DCM of the Sawtooth Valley lakes from June to October 1993 were 120–1000% higher than those in the epilimnia (Table 2).

Fig. 2. Mean chlorophyll *a* concentration (µg/L) in the epilimnion ($n = 3$) and at the 1% light level ($n = 2$) in Redfish Lake, 1993. Vertical bars show range.

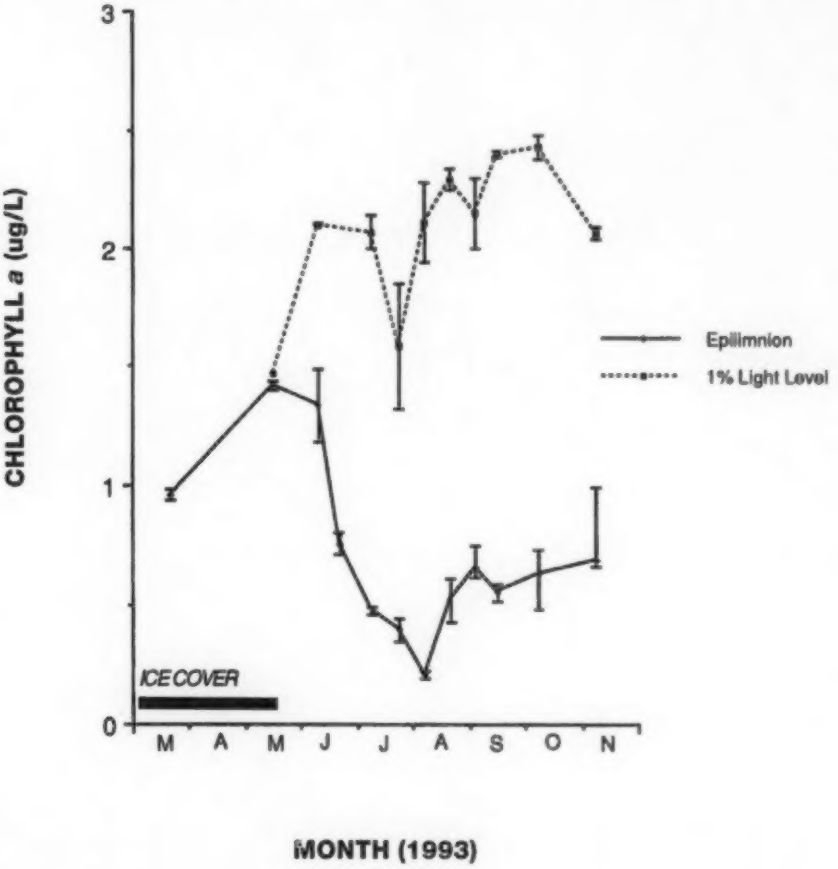


Fig. 3. Seasonal changes in the biovolumes of different phytoplankton taxa in Redfish Lake, 1993: (*a*) epilimnetic water and (*b*) at the 1% light level.

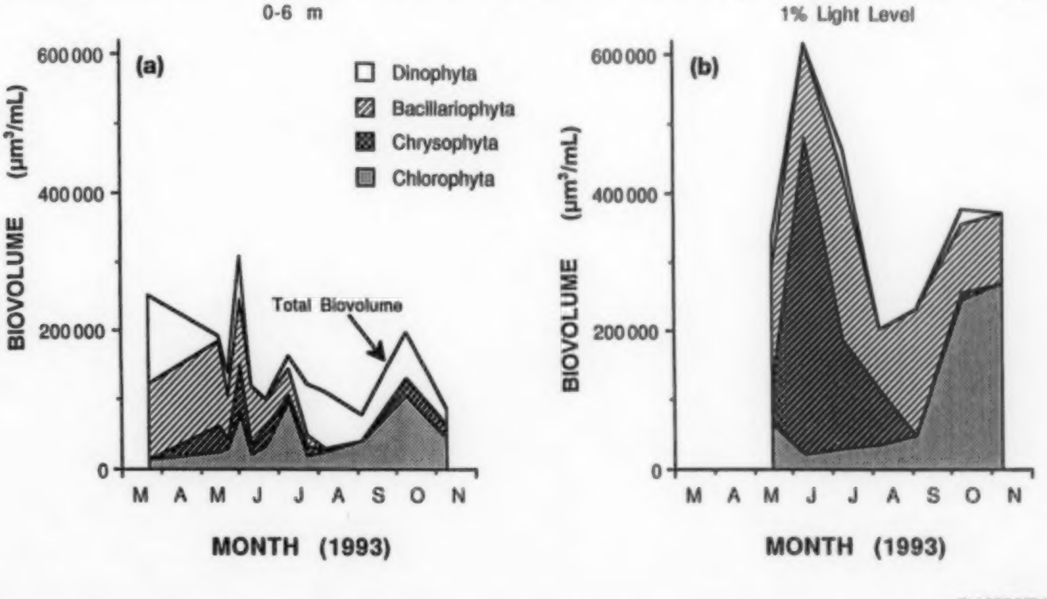


Fig. 4. Vertical profiles of primary productivity (PPR) and temperature in the Redfish, Pettit, Alturas, and Stanley lakes in 1993. Mean and range of duplicate measurements are shown. Curves for PPR are fit with spline functions.

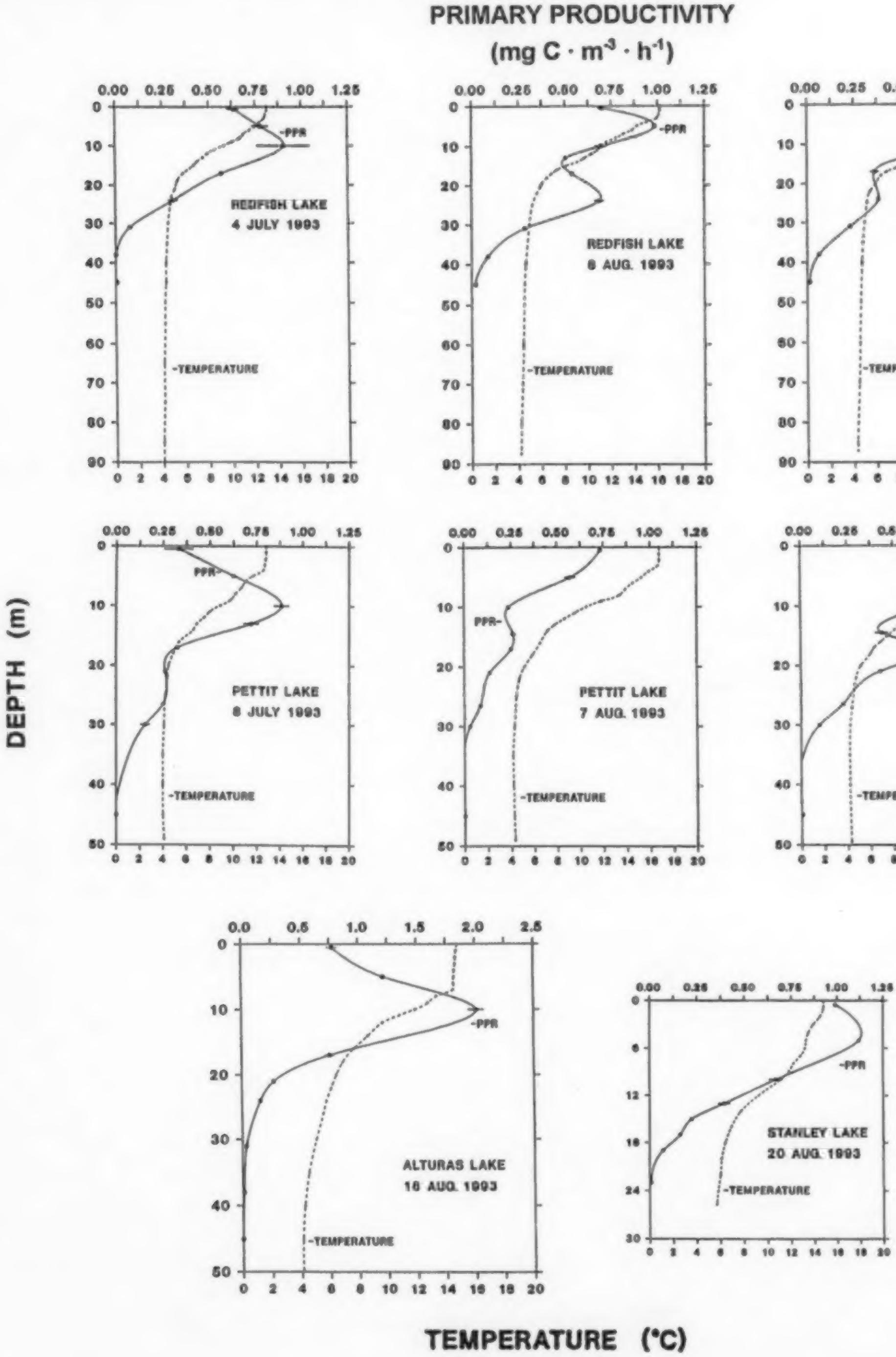
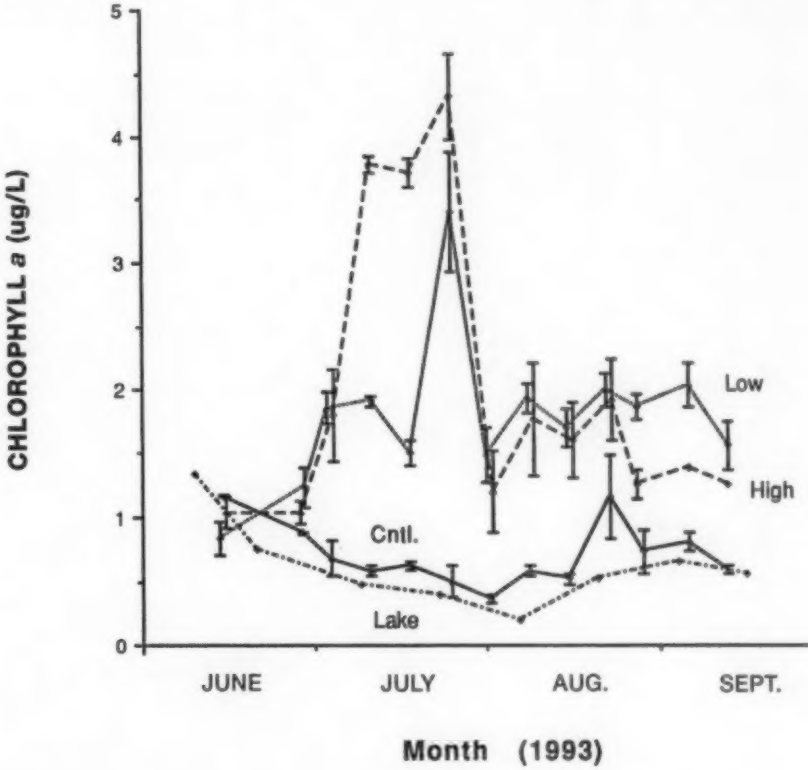


Fig. 5. Mean chlorophyll *a* (μg/L) from epilimnetic tube samples (0–6 m) collected from Redfish Lake limnocorrals, 1993. Control (CNTL), low, and high fertilization treatments are shown. Lake epilimnetic chlorophyll *a* (μg/L) is also shown for comparison. Vertical bars for limnocorrals show ranges ($n = 2$).



The seasonal progression of epilimnetic chlorophyll *a* in the Sawtooth Valley lakes in 1993 was similar to that of Redfish Lake: the highest values for the ice-free season occurred just after spring overturn in May, followed by a gradual decline to a midsummer minimum, after which levels increased (Fig. 2). At the 1% light level, however, chlorophyll *a* increased irregularly after spring overturn in each lake (as exemplified by Redfish Lake in Fig. 2; also see Gross (1995) for similar figures for the other Sawtooth Valley lakes).

Not only were chlorophyll *a* concentrations higher near the 1% light level, but greater algal biovolumes were supported there as well (Fig. 3). In Redfish Lake, for example, biovolumes were on the average 170% greater at the 1% light level than in the epilimnion.

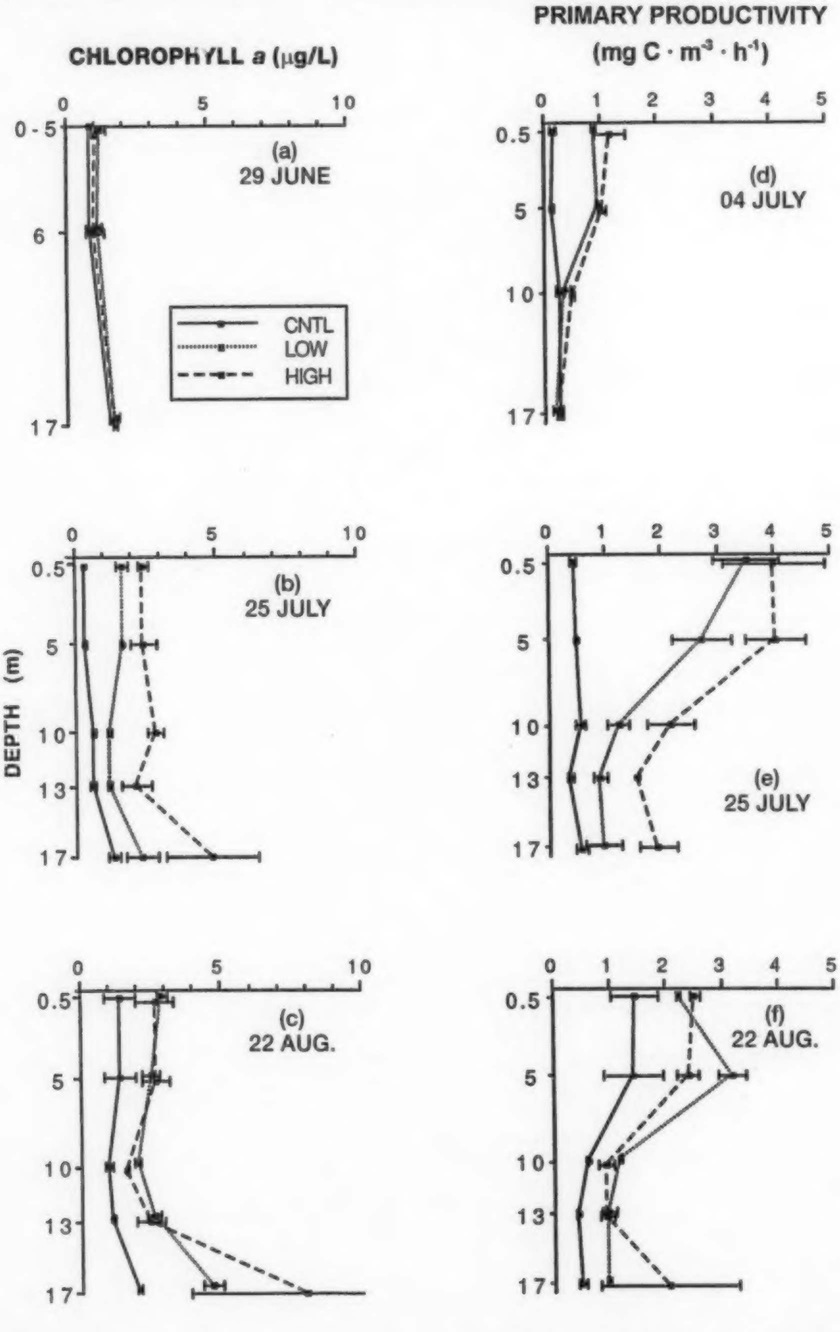
Diatoms (*Synedra*, *Cyclotella*, *Melosira*, and *Tabellaria*) and *Dinobryon* sp. dominated the lake's epilimentic biovolume early in the growing season. By late July, however, the diatoms declined in the epilimnia, and were replaced by chlorophytes and dinophytes, particularly *Peridinium* (Fig. 3). Cyanobacteria were rare in all lakes (<3% of mean summer epilimnetic biovolume) except in Alturas, where they were present but nondominant (13%).

In Redfish Lake, the chrysophyte *Dinobryon* sp. and the diatoms *Synedra* sp. and *Tabellaria* sp. made up a considerable portion of the biovolume of the deep algal stratum (Fig. 3). Diatom and *Dinobryon* sp. peaks occurred later in the DCM than in the epilimnion. In the other Sawtooth Valley lakes, the deep algal stratum consisted primarily of *Oocystis* and *Chlorella* spp. (Gross 1995).

Rates of primary production in the Sawtooth Valley lakes were very low, with most of the production occurring below the epilimnion. Integrated water column productivity ranged from 9 to 27 mg $C \cdot m^{-2} \cdot h^{-1}$ on the eight occasions it was measured. In Redfish Lake, 68–72% of the primary production occurred below the epilimnion. In the other Sawtooth Valley lakes, except Stanley, ≥62% of the primary production occurred below the epilimnia (Fig. 4). Because of Stanley Lake's shallower depth and smaller non-epilimnetic photic volume, most of the PPR (64%) occurred in its epilimnion. Photosynthesis was measurable in all lakes to depths of at least 30 m, except in Stanley Lake, which is only 26 m deep (Table 1).

The primary production peak usually occurred near the top of the thermocline at depths of 5–10 m (Fig. 4). Lowered productivity at the surface (photoinhibition) was observed in all profiles, except for Pettit Lake on 7 August, which was an overcast, stormy day. Secondary peaks in productivity in the metalimnion were found on two of three dates in Redfish Lake, and on all three dates we made measurements in Pettit Lake. In Alturas and Stanley lakes, secondary peaks in productivity were absent on the days measurements were taken, but both analyses were done on partially cloudy days.

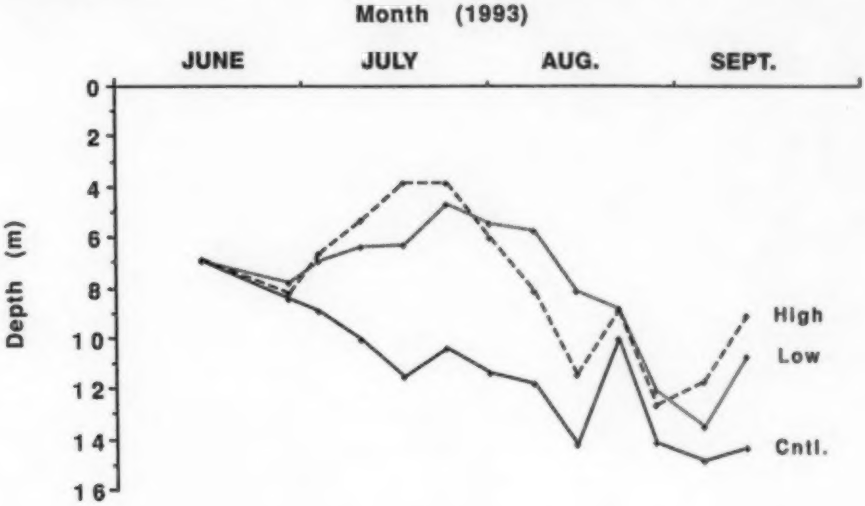
Fig. 6. Vertical profiles of (*a–c*) mean chlorophyll *a* (µg/L) and (*d–f*) primary productivity (mg $C \cdot m^{-3} \cdot h^{-1}$) in the Redfish Lake limnocorrals, 1993. Control (CNTL), low, and high fertilization treatments are shown; horizontal bars show ranges ($n = 2$).



Limnocorral experiment

Nutrient additions to the limnocorrals caused a significant increase in chlorophyll (repeated measures ANOVA, $F_{2,3} = 57.8$, $p = 0.004$). The means (and ranges) of the weekly epilimnetic chlorophyll levels were 0.65 (0.36–1.16), 1.94 (1.49–3.41), and 2.19 (1.20–4.32) µg/L for the CNTL, LOW, and HIGH treatments, respectively (Fig. 5). Although there was an overall significant treatment effect, the LOW and HIGH means were not significantly different from each other (post hoc Tukey's comparison, $\alpha = 0.05$). The epilimnetic chlorophyll levels in the CNTL treatments followed a trend similar to, although slightly higher than, the lake during the experiment (Fig. 5).

Fig. 7. Mean Secchi depth ($n = 2$) by treatment in the Redfish Lake limnocorrals for the duration of the experiment. Control (CNTL), low, and high fertilization treatments are shown.



The nutrient additions caused increased chlorophyll at all depths, particularly at 17 m (Figs. 6*a*–6*c*). The high concentrations at 17 m may have been an artifact of the 17-m depth boundary imposed by the limnocorral bottoms. Samples collected from 17 m may have contained some phytoplankton that had sedimented out of the water column.

Nutrient additions to the limnocorrals significantly stimulated primary production (repeated measures ANOVA, $F_{2,3} = 75.6$, $p = 0.003$). Fertilization significantly increased epilimnetic production more than metalimnetic production (Figs. 6*d*–6*f*) (repeated measures ANOVA, $F_{3,9} = 19.9$, $p < 0.001$). Six days after the experiment began (4 July), increased production in the epilimnia of both the LOW and HIGH treatments was apparent (ANOVA, $F_{2,3} = 9.16$, $p = 0.053$). Metalimnetic production rates, however, were similar in the control and fertilized treatments. Three weeks later (25 July), epilimnetic production was further stimulated in both the LOW and HIGH treatments (ANOVA, $F_{2,3} = 146$, $p = 0.001$), and the effects extended into the metalimnia. After four additional weeks (22 August), primary production was still enhanced by the nutrient additions (ANOVA, $F_{2,3} = 8.82$, $p = 0.055$), but the differences among treatments were less distinct.

When we integrated the phytoplankton productivity profiles through the water column, we found that nutrient additions significantly increased primary production by 110–290% in the LOW treatment, and by 90–490% in the HIGH (repeated measures ANOVA, $F_{2,3} = 51.1$, $p = 0.005$). A post hoc Tukey's comparison, however, showed that the increases in primary productivity resulting from the LOW and HIGH treatments were not significantly different from each other ($\alpha = 0.05$).

Water transparency, as measured by Secchi depth, was significantly decreased by the nutrient additions (repeated measures ANOVA, $F_{2,3} = 57.6$, $p = 0.004$). The means of the weekly Secchi depth measurements were 11.3, 8.0, and 7.9 m for the CNTL, LOW, and HIGH treatments, respectively (Fig. 7). The LOW and HIGH Secchi means were significantly different from the CNTL Secchi mean but not significantly different from each other (post hoc Tukey's comparison, $\alpha = 0.05$).

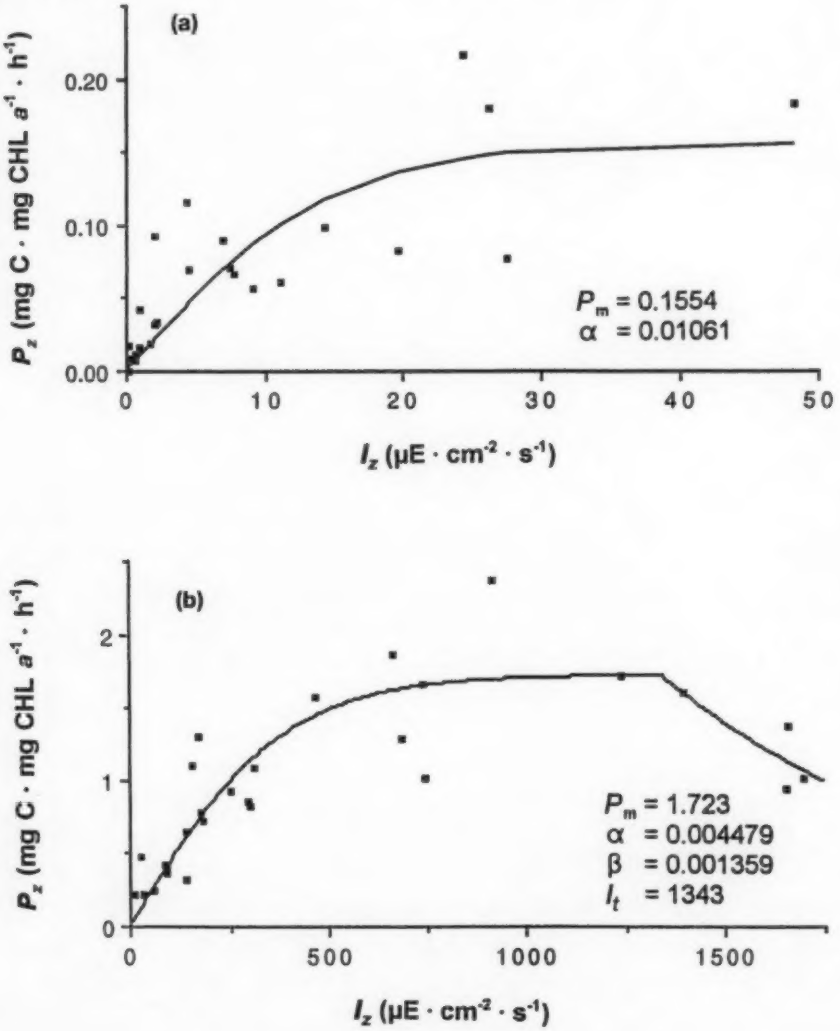
Table 3. Mean light extinction coefficients, percentage of surface light at 17 m depth, and percentage shading in nutrient treatments (LOW and HIGH) compared with the control (CNTL) treatments for the Redfish Lake limnocorrals, 1993.

Treatment	Mean light extinction coefficient	% of surface light at 17 m depth	% less light at 17 m than in CNTL treatment
	4 July 1993 ($p = 0.697$)		
CNTL	0.241*a*	1.68	—
LOW	0.247*a*	1.53	9
HIGH	0.237*a*	1.81	–8
	11 July 1993 ($p = 0.264$)		
CNTL	0.242*a*	1.69	—
LOW	0.266*a*	1.10	35
HIGH	0.268*a*	1.06	37
	25 July 1993 ($p = 0.068$)		
CNTL	0.188*a*	4.17	—
LOW	0.223*b*	2.27	46
HIGH	0.221*b*	2.48	41
	9 August 1993 ($p = 0.080$)		
CNTL	0.197*a*	3.53	—
LOW	0.221*b*	2.36	33
HIGH	0.212*ab*	2.76	22

Note: Light extinction coefficients followed by the same letter were not significantly different (Tukey's post hoc comparison with $\alpha = 0.10$). The p values for the dates are from ANOVAs (df = 2) for each date (Gross 1995).

The LOW and HIGH treatments had 22–46% less light available at 17 m depth than did the CNTL treatments on 11 July, 25 July, and 9 August (Table 3). When using a post hoc Tukey's comparison and $\alpha = 0.10$, these differences in light were significantly different for 25 July ($p = 0.07$) and

Fig. 8. Relationship between irradiance (I_z) and photosynthetic rates normalized to chlorophyll *a* (CHL *a*)(P_z) from six 1993 dates in the Sawtooth Valley lakes. The curve in *a* was fit through data points measured below the bottom of the thermocline using the method of Neale and Richerson (1987). The curve in *b* was fit through data points measured above the bottom of the thermocline using the method of Jassby and Platt (1976). The curves were used to predict primary production depth profiles under fertilized and unfertilized conditions in Redfish Lake. Data are from Gross (1995).

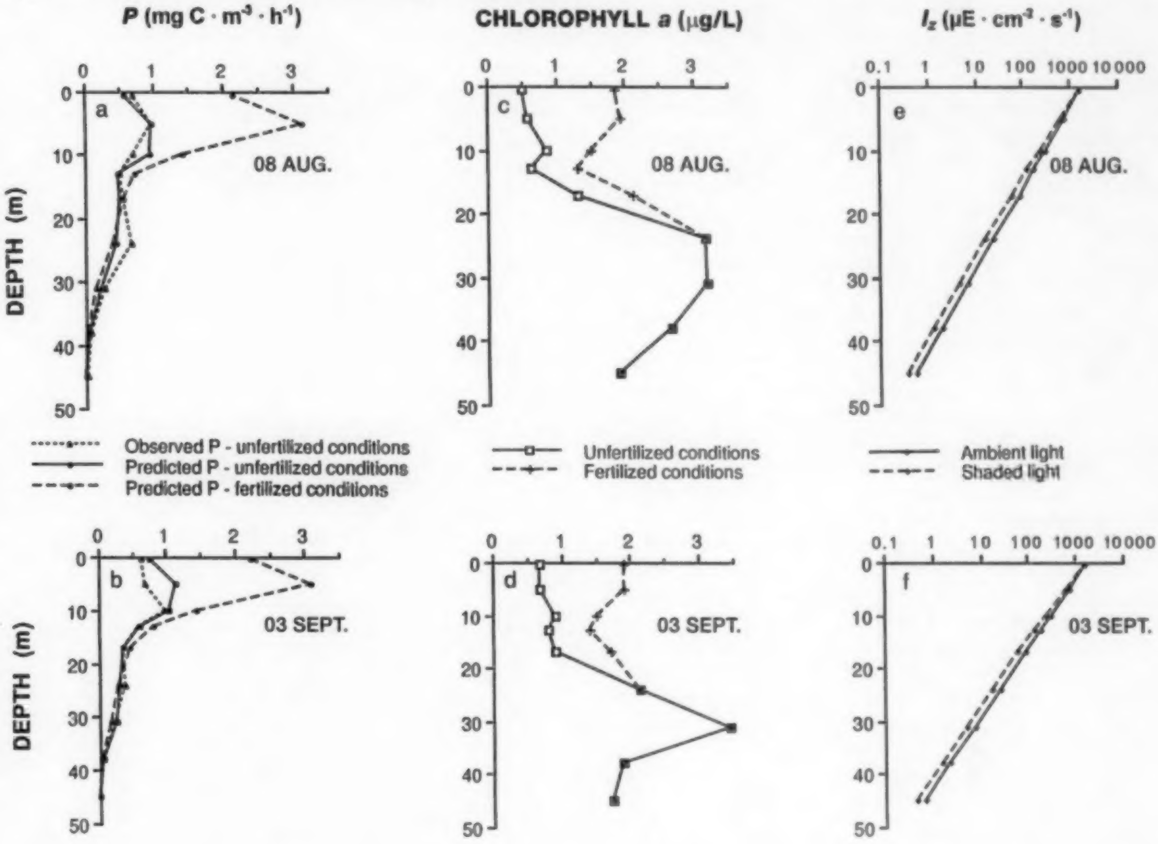


9 August ($p = 0.08$), but not for 11 July ($p = 0.26$). Measurement of the light profiles was problematic owing to shading caused by infrastructure supporting the limnocorrals (e.g., docks, float tubes, sampling platforms), and this contributed to the variability in the light data. Nevertheless, it is apparent from the light, Secchi, and chlorophyll data that substantial shading was caused in the limnocorrals by the nutrient additions.

Primary productivity predictions

The results of the lake sampling, the limnocorral experiment, and the *P–I* curves (Fig. 8) were used to predict primary production (PPR) depth profiles under fertilized and unfertilized conditions for two dates in Redfish Lake (Fig. 9). The predictions were made using a range of light extinction coefficients from Table 3. By using a range of light coefficients in eq. 3, the sensitivity of this modelling approach to different levels of shading was tested. A low level of shading in the fertilized versus unfertilized scenario was modelled using LE_{high} (0.212) and LE_{cntl} (0.197) from 9 August 1993; intermediate shading was modelled using LE_{low} (0.221) and LE_{cntl} (0.197) from 9 August 1993; high shading was modelled using LE_{low} (0.223) and LE_{cntl} (0.188) from 25 July 1993. Under the low, intermediate, and high shading scenarios, 22, 33, and 46% less light, respectively, was available at the 17-m depth in the fertilized versus unfertilized scenario.

Fig. 9. Primary production profiles for Redfish Lake on two dates in 1993. (*a* and *b*) Observed and predicted primary production (*P*) profiles under fertilized and unfertilized conditions using intermediate shading levels. (*c* and *d*) Chlorophyll *a* concentrations observed in the lake under unfertilized conditions and predicted for fertilized conditions. (*e* and *f*) Light levels (I_z) observed in the lake under ambient conditions and predicted for fertilized conditions under intermediate shading levels.



The simulations demonstrated a large increase in epilimnetic PPR owing to fertilization and only a slight decrease in production in the deeper strata because of self-shading (Fig. 9). Depending on the level of shading used, the simulations predicted integrated water column PPR for fertilized conditions to be 183–201% of predicted PPR for unfertilized conditions for 8 August and 175–190% for 3 September. Predicted integrated PPR for unfertilized conditions was 91 and 117%, respectively, of the actual PPR observed in the lake on 8 August and 3 September.

Discussion

Our results demonstrate that there are broad DCM in the Sawtooth Valley lakes and that higher phytoplankton biovolumes are present in these DCM than in the lake's epilimnetic waters. Furthermore, these deeper waters contribute over 60% of the primary productivity in the lakes.

The limnocorral experiment demonstrated that lake fertilization at the levels tested would decrease water clarity and increase shading of the DCM, thus compressing the photic zone. However, our modelling indicated that the resulting loss of primary production in the DCM under these fertilized conditions would be more than offset by higher productivity in the epilimnion. Primary production in the 17-m water column of the treated limnocorrals was 90–490% greater than that in the controls.

Compression of the photic zone in association with cultural eutrophication has been documented in other lakes. Coastal British Columbian sockeye-rearing lakes that received nutrient additions had shallower Secchi depths than unfertilized lakes (Stockner 1987). Goldman (1988) showed that water transparency decreased and the photic zone compressed during the onset of cultural eutrophication of ultra-oligotrophic Lake Tahoe. He also found that water column primary productivity rates increased as Secchi depth decreased.

For lake fertilization to help in the recovery of the Snake River sockeye salmon, nutrient additions must stimulate the zooplankton that occupy waters in which sockeye salmon reside, thus allowing the energy captured in increased PPR to be transferred to the juvenile sockeye. Because juvenile sockeye often avoid water temperature >16°C (Foerster 1968), Shortreed and Stockner (1990) concluded that the effectiveness of surface fertilization of Sproat Lake (a British Columbia lake with a DCM) might be reduced because the zooplankton there did not display diel vertical migrations. Thus, the epilimnetic zooplankton that would benefit from nutrient additions would not be available to the juvenile sockeye. These concerns are less applicable to Redfish Lake. The distribution of zooplankton in Redfish Lake's water column suggests that they may be able to convey energy gains resulting from epilimnetic nutrient additions to juvenile sockeye (Steinhart et al. 1994). Also, epilimnetic temperatures in Redfish Lake exceeded 16°C for a much shorter period of the year than in Sproat Lake, and thus the epilimnetic zooplankton should be more available to the sockeye salmon.

An approach that might circumvent spatial and temporal concerns about juvenile sockeye habitation of the water column is to inject nutrient additions into deeper waters (metalimnetic fertilization) (LeBrasseur et al. 1978; Gross 1995). This approach may be more effective than surface fertilization in facilitating sockeye growth.

Although our studies were not specifically designed to isolate mechanisms responsible for the DCM's presence, we may have identified a factor contributing to their maintenance in the Sawtooth Valley lakes. With the onset of thermal stratification following spring overturn in 1993, stream inflow temperatures (automatically logged every 36 min) were almost always colder than lake epilimnetic temperatures (H.P. Gross and W.A. Wurtsbaugh, unpublished data). Based on temperature, we estimated that the inflow water would plunge to the meta- or hypo-limnion during most of the ice-free season. Diel fluctuations in the stream temperatures indicated that the entering stream water may plunge across a wide range of depths on a given day. Fluoroscene dye tracer studies in the Sawtooth Valley lakes have confirmed the plunging inflow phenomenon (W.A. Wurtsbaugh, unpublished data), although dye entering the lake did not plunge as deeply as temperature alone would predict. Nevertheless, it appears that nutrients brought into the lake through inflow streams during the ice-free stratified period (the primary nutrient input source to lakes during this time) are first delivered to metalimnetic and hypolimnetic waters. This may result in higher nutrient concentrations in these deeper waters than in the lakes' epilimnetic waters, thus contributing to the maintenance of the DCM.

During the second half of our limnocorral experiment, the HIGH treatments did not significantly influence primary productivity, epilimnetic chlorophyll *a*, or Secchi depth more than did the LOW treatments ($p > 0.5$). These results were unexpected but may have been caused by differences in periphyton between the LOW and HIGH treatments. Periphyton chlorophyll *a* in the HIGH treatments was 90–720% greater than in the LOW treatments (Budy et al. 1994). The periphyton growth in the HIGH treatments most likely deprived the phytoplankton of more added nutrients than did periphyton in the LOW treatments, thus diminishing the difference in primary productivity between the two treatments.

In conclusion, decreases in light and increases in primary production should be expected as a result of fertilization of ultra-oligotrophic, dimictic Redfish Lake. Decreased PPR in the DCM would be more than offset by increased PPR in the epilimnetic waters. For lake fertilization to be used as a tool to assist in the Snake River sockeye salmon recovery effort, energy captured in increased PPR must be effectively transferred to the zooplankton, and ultimately to the juvenile sockeye salmon, without causing adverse effects on the aquatic community and trophic structure of the Sawtooth Valley lakes.

Acknowledgments

We are indebted to the following people for contributing to this work: T. Blenckner, G. Steinhart, S. Durham, D. Staab, D. Hunter, N. Bouwes, N. Roberts, and J. Ruzycki. P. Neale provided data and advice. Funding was provided through the Shoshone–Bannock Indian Tribes (from the Bonneville Power Administration), a Vice-Presidential Fellowship from Utah State University, and the Ecology Center at Utah State University. In addition, we would like to acknowledge invaluable logistic support from C. Draper and the staff of the Stanley Ranger Station (Sawtooth National Recreation Area) and the Sawtooth Fish Hatchery (Idaho Fish and Game).

References

Anderson, G.C. 1969. Subsurface chlorophyll maximum in the northeast Pacific Ocean. Limnol. Oceanogr. **14**: 386–391.

Beauchamp, D.A., Budy, P.E., Wurtsbaugh, W.A., Gross, H.P., Luecke, C., and Spaulding, S. 1993. Hydroacoustic assessment of fish abundance in Sawtooth Valley lakes. *In* Snake River sockeye salmon (*Oncorhynchus nerka*) habitat/limnologic research—annual report 1992. *Edited by* S. Spaulding. Publ. No. DOE/BP-22548-1. U.S. Department of Energy, Bonneville Power Administration, Portland, Oreg. pp. 53–71.

Bevan, D., Harville, J., Bergman, P., Bjornn, T., Crutchfield, J., Klingerman, P., and Litchfield, J. 1994. Snake River salmon recovery team: final recommendations to National Marine Fisheries Service. National Marine Fisheries Service, Portland, Oreg.

Budy, P., Luecke, C., Wurtsbaugh, W.A., and Gross, H.P. 1994. Effects of nutrient enhancement on plankton and the growth of juvenile salmon in Redfish Lake. *In* Snake River sockeye salmon habitat and limnological research—annual report 1993. *Edited by* D. Tuescher, D. Taki, W.A. Wurtsbaugh, C. Luecke, P. Budy, H.P. Gross, and G. Steinhart. Publ. No. DOE/BP-22548-2. U.S. Department of Energy, Bonneville Power Administration, Portland, Oreg. pp. 62–77.

Budy, P., Luecke, C., Wurtsbaugh, W.A., Gross, H.P., and Gubala, C. 1995. Limnology of the Sawtooth Valley lakes with respect to potential growth of juvenile Snake River sockeye salmon. Northwest Sci. **69**: 33–150.

Crumpton, W.G. 1987. A simple and reliable method for making permanent mounts of phytoplankton for light and fluorescence microscopy. Limnol. Oceanogr. **32**: 1154–1159.

Fee, E.J. 1976. The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, northwestern Ontario: implications for primary production estimates. Limnol. Oceanogr. **21**: 767–783.

Foerster, R.E. 1968. The sockeye salmon, *Oncorhynchus nerka*. Bull. Fish. Res. Board Can. No. 162.

Goldman, C.R. 1988. Primary productivity, nutrients, and transparency during the early onset of eutrophication in ultra-oligotrophic Lake Tahoe, California–Nevada. Limnol. Oceanogr. **33**: 1321–1333.

Gross, H.P. 1995. Evaluation of lake fertilization as a tool to assist in the recovery of the Snake River sockeye salmon. M.S. thesis, Utah State University, Logan, Utah.

Gross, H.P., Wurtsbaugh, W.A., Luecke, C., and Budy, P. 1994. Comparison of epilimnetic and metalimnetic fertilizations on the phytoplankton and zooplankton in Pettit Lake, Idaho. *In* Snake River sockeye salmon habitat and limnological research—annual report 1993. *Edited by* D. Tuescher, D. Taki, W.A. Wurtsbaugh,

C. Luecke, P. Budy, H.P. Gross, and G. Steinhart. Publ. No. DOE/BP-22548-2. U.S. Department of Energy, Bonneville Power Administration, Portland, Oreg. pp. 78–99.

Hobson, L.A., and Lorenzen, C.J. 1972. Relationship of chlorophyll maxima to density structure in the Atlantic Ocean and Gulf of Mexico. Deep-Sea Res. **19**: 297–306.

Holm-Hansen, O., and Riemann, B. 1978. Chlorophyll *a* determination: improvements in methodology. Oikos, **30**: 438–447.

Jassby, A.D., and Platt, T. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr. **21**: 540–547.

Kiefer, D.A., Olson, R.J., and Holm-Hansen, O. 1976. Another look at the nitrite and chlorophyll maxima in the central North Pacific. Deep-Sea Res. **23**: 1199–1208.

Kyle, G.B., Koenings, J.P., and Barret, B.M. 1988. Density-dependent, trophic level responses to an introduced run of sockeye salmon (*Oncorhynchus nerka*) at Frazer Lake, Kodiak Island, Alaska. Can. J. Fish. Aquat. Sci. **45**: 856–867.

LeBrasseur, R.J., McAllister, C.D., Barraclough, W.E., Kennedy, O.D., Manzer, J., Robinson, D., and Stephens, K. 1978. Enhancement of sockeye salmon (*Oncorhynchus nerka*) by lake fertilization in Great Central Lake: summary report. J. Fish. Res. Board Can. **35**: 1580–1596.

Luecke, C., Budy, P., Wurtsbaugh, W.A., Gross, H.P., and Steinhart, G. 1996. Simulated growth and production of endangered Snake River sockeye salmon: assessing lake management strategies for nursery lakes. Fisheries (Bethesda), **21**(6): 18–25.

Moll, R.A., and Stoermer, E.F. 1982. A hypothesis relating trophic status and subsurface chlorophyll maxima of lakes. Arch. Hydrobiol. **94**: 425–440.

Neale, P.J., and Richerson, P.J. 1987. Photoinhibition and the diurnal variation of phytoplankton photosynthesis—I. Development of a photosynthesis–irradiance model from studies of in situ response. J. Plankton Res. **9**: 167–193.

Platt, T., Harrison, W.G., Irwin, B., Horne, E.P., and Gallegos, C.L. 1982. Photosynthesis and photoadaptation of marine phytoplankton in the Arctic. Deep-Sea Res. **29**: 1159–1170.

Reynolds, C.S. 1984. The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge, England.

SAS Institute Inc. 1988. SAS/STAT user's guide, release 6.03 edition. SAS Institute Inc., Cary, N.C.

Schindler, D.W. 1977. Evolution of phosphorous limitation in lakes. Science (Washington, D.C.), **195**: 260–262.

Shortreed, K.S., and Stockner, J.G. 1990. Effect of nutrient additions on lower trophic levels of an oligotrophic lake with a seasonal deep chlorophyll maximum. Can. J. Fish. Aquat. Sci. **47**: 262–273.

Steele, J.H. 1964. A study of production in the Gulf of Mexico. J. Mar. Res. **22**: 211–222.

Steinhart, G., Gross, H.P., Budy, P., Luecke, C., and Wurtsbaugh, W.A. 1994. Limnological investigations and hydroacoustic surveys of Sawtooth Valley lakes. *In* Snake River sockeye salmon habitat and limnological research—annual report 1993. *Edited by* D. Tuescher, D. Taki, W.A. Wurtsbaugh, C. Luecke, P. Budy, H.P. Gross, and G. Steinhart. Publ. No. DOE/BP-22548-2. U.S. Department of Energy, Bonneville Power Administration, Portland, Oreg. pp. 30–61.

Stockner, J.G. 1987. Lake fertilization: the enrichment cycle and lake sockeye salmon (*Oncorhynchus nerka*) production. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 198–215.

Stockner, J.G., and Shortreed, K.S. 1988. Response of *Anabaena* and *Synechococcus* to manipulation of nitrogen:phosphorus ratios in a lake fertilization experiment. Limnol. Oceanogr. **33**: 1348–1361.

Wetzel, R.G. 1983. Limnology. Saunders College Publishing, New York, N.Y.

Wetzel, R.G., and Likens, G.E. 1991. Limnological analyses. Springer-Verlag, New York, N.Y.

PERSPECTIVES

The Laurentian Great Lakes experience: a prognosis for the fisheries of Atlantic Canada

S.R. Kerr and R.A. Ryder

Abstract: The fish production systems of Atlantic Canada are in a state of crisis, in the social, political, economic, and biological senses. We doubt that the true scope and provenance of the crisis have yet been apprehended by the responsible managers. Our view is that the obvious overfishing that precipitated the problem is but the first major instance of further devastation that will visit the fishery. We find numerous parallel behaviours among the various Atlantic fisheries and the patterns of demise of the fish production systems of the Great Lakes basin ecosystem. Unless management regimes awaken to these realities, the fisheries of Atlantic Canada are doomed to the same dismal scenarios as were witnessed in the Great Lakes. Properly understood, remedial measures painfully learned in the Great Lakes could usefully inform responsible management agencies in Atlantic Canada. A new institutional structure is required in Atlantic Canada to deal with the requirements of ecosystem management.

Résumé : Les systèmes de production piscicole du Canada atlantique sont dans un état de crise, au sens social, politique, économique et biologique. Nous doutons que les gestionnaires responsables soient parvenus à comprendre l'ampleur réelle et l'origine de la crise. Nous estimons que la surpêche évidente qui a précipité la crise n'est que le premier des grands fléaux qui s'abattront sur cette pêcherie. Nous trouvons de nombreux parallèles entre les problèmes des diverses pêcheries de l'Atlantique et l'effondrement des systèmes de production piscicole dans l'écosystème du bassin des Grands Lacs. À moins que les responsables de la gestion prennent conscience de ces réalités, les pêcheries de l'Atlantique sont condamnées à connaître le même triste sort que celles des Grands Lacs. Bien comprises, les mesures de remise en état douloureusement apprises dans les Grands Lacs pourraient éclairer utilement les organismes responsables de la gestion dans le Canada atlantique. Une nouvelle structure institutionnelle s'impose dans cette région pour faire face aux exigences de la gestion de l'écosystème.

[Traduit par la Rédaction]

Introduction

The Atlantic fisheries of Canada have entered a period of crisis. The demersal fisheries in particular have been devastated by overfishing, both domestic and foreign, possibly exacerbated by intrusions of anomalously cold water masses, substantial changes in the abundances of important prey species, and conceivably by other factors that remain to be confirmed. Informed observers are far from agreement as to the precise balance of causes that contributed to the disaster, but few dispute that overfishing was the proximate and sufficient cause (Hutchings and Myers 1994).

Our expectation is that the current disaster, precipitated by overexploitation of Atlantic Canadian fish stocks, marks merely the first stage of an impending series of problems that will visit these fisheries in the next few decades. From our scientific perspective, derived over lengthy professional careers that have encompassed both the Laurentian Great Lakes and Atlantic Canadian fisheries, it is an instance (to quote Yogi Berra) of "Déjà vu, all over again". We view the developing situation in Atlantic Canada as familiar ground that was first experienced decades ago in the Great Lakes. The spatial and temporal scales of the experiences are clearly different, as are many of the details, such as those concerning extirpation of various taxa (species, subspecies, races, etc.) of fish stocks, but the net effect remains substantially the same; the fisheries of Atlantic Canada are being destroyed at the same remarkable rate as characterised the Great Lakes fisheries three or four decades ago. We argue in what follows that the Great Lakes experiences serve as prototypes for the sequence of events that has begun to unfold in Atlantic Canada.

Our purpose in providing this perspective on the common problems that were witnessed first on the Great Lakes, and are now being seen in Atlantic Canada, is founded in the hope that history does not necessarily have to repeat itself, although our expectation is that it will. Neither society in general, nor its relevant political and social institutions, are positioned to learn from historical precedent established in a different ecological and sociopolitical milieu because there are effective disciplinary, institutional, and jurisdictional barriers that obviate our

Received October 22, 1996. Accepted March 27, 1997.
713

S.R. Kerr.[1] Biology Department, Dalhousie University, Halifax, NS B3H 4J1, Canada.
R.A. Ryder. Ontario Ministry of Natural Resources, Aquatic Ecosystems Science Section, Peterborough, ON K9J 8N1, Canada.

[1] Author to whom all correspondence should be addressed. e-mail: skerr@ac.dal.ca

ability to profit from the lessons of history. What quirk of human nature makes it so difficult for us to learn from the failures of others?

It is plausible to suppose that the fisheries of Atlantic Canada, as we recently knew them, may disappear forever. It is reasonable to suppose that their replacement will constitute an eclectic, opportunistic mix of commercial opportunities that will soon supplant our collective memories of what the fishery was, and should have remained. This is precisely the path that was followed in the Laurentian Great Lakes, and there is no reason to suppose that the Atlantic fisheries will follow some different course. That is, unless the lessons of history are assimilated by the management regime, and by society in general, Canada's Atlantic fisheries are destined to revisit the experiences of our "inland oceans", the Laurentian Great Lakes.

The Great Lakes precedent

The sequence of events that began to unfold in the Laurentian Great Lakes ecosystem many decades ago, and reached a critical stage in the 1950s and 1960s, can be reexamined with considerable profit. The conventional wisdom at the time embraced several basic tenets.

One view that prevailed at the time was that fish were such extravagently fecund organisms that (recruitment) overfishing was not possible. The assumption was based on the theoretical supposition that because only a small spawning stock biomass is required to replenish a fish stock, the fishing effort needed to eradicate that small remnant would not be economically feasible, and the stock would therefore recover. Apparently this notion remains in contention even now (MacKenzie 1995), but as events by the 1960s would show, conventional wisdom was tragically wrong, owing to a profound misunderstanding of the behaviours of both fish and fishers. This is not the place to expound upon these misapprehensions, but in brief, fishes form aggregations for various purposes that are extremely vulnerable to modern fishing methods (Hutchings 1996). Experience proves that modern fishing technology is economically capable of locating and fishing out every last aggregation. In rapid order, this process of search and destroy on the Great Lakes led to the loss of literally dozens of phenotypically and perhaps genetically (appropriate technology did not exist at the time to test this dimension) distinct stocks of coregonines (e.g., subgenus *Leucichthys*) and the salmonine genus *Salvelinus* that once supported valuable fisheries. The most conspicuous losses were various subspecies, races, or phenotypic stocks of lake trout (*Salvelinus namaycush*), coaster brook trout (*Salvelinus fontinalis*), and most varieties of deepwater ciscoes, as well as the blue pike (*Stizostedion vitreum glaucum*) of Lake Erie, which passed in the course of little more than a decade from being the largest and most valuable fishery of the Great Lakes to becoming virtually extinct through severe reductions in numbers and subsequent genetic introgression with the closely related walleye (*Stizostedion vitreum vitreum*). The two-phased process was a direct result of overexploitation (Parsons 1967; Regier et al. 1969).

An additional conventional wisdom that prevailed in the 1950s and into the early 1960s was that the Great Lakes were themselves so vast, and their capacities for dilution so enormous, that the risk of anthropogenic harm to the Great Lakes themselves did not exist (Smith 1972). To be sure, it was generally acknowledged that localised, inshore effects might be experienced in harbours, small embayments, and the delta areas of tributaries but the offshore waters were themselves thought to be immune to habitat degradation. Nevertheless, by the 1960s, newspaper headlines were proclaiming (quite inaccurately) that Lake Erie was either "dead" or "dying" (Smith 1962). For example, the bottom waters of the large Central Basin of Lake Erie became completely anoxic and the previously abundant mayflies (*Hexagenia limbata*) were eliminated, as well as a host of other invertebrates and fishes (Carr 1962). The pronouncements of death were ill-founded, but the profound changes in character of the living biota and their habitats were remarkable, and quite unwelcome from a human perspective. The cultural eutrophication process in the Great Lakes became recognised as a system-wide problem needing urgent redress (Vallentyne 1974). In addition to the widespread problem of nutrient introductions was the associated input of xenobiotic and other contaminants, which had the effect of rendering components of the biota unsafe for human consumption. This effect was exacerbated through bioaccumulation and biomagnification at the higher trophic levels that also included the human population. Habitat modification, particularly in the form of shoreline and riparian "development", accelerated the removal of critical spawning and nursery areas (Francis et al. 1979), a process begun much earlier in the course of human deforestation and settlement of the Great Lakes basins (Sly 1991).

There was also the ubiquitous problem of species introductions. Being a young (less than 10 000 years B.P.) and therefore depauperate ecosystem, the Great Lakes are, presumably, correspondingly vulnerable to colonisation by exotic species. The risk associated with introductions, such as the spectacular harm associated with the sea lamprey (*Petromyzon marinus*), rainbow smelt (*Osmerus mordax*), dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*) and many other species that were either accidentally or deliberately introduced, was recognised early on, although relatively little was done initially to control the problem. Mills et al. (1993) have documented the introduction of 139 species of nonindigenous flora and fauna, of which at least 13 species have significantly affected the economic and ecological performance of the Great Lakes ecosystem. The current configuration of the ichthyofauna comprises an eclectic mixture of a few native species, and a variety of accidentally and deliberately introduced species that are self-sustaining, augmented by hatchery-supported assemblages of certain exotic salmonines (e.g., coho salmon (*Oncorhynchus kisutch*)), which are largely unfit for human consumption, owing to their proclivity for accumulating toxic body burdens of contaminants (DeVault and Weishaar 1983, 1989). Ironically, the lesson of this sorry story has apparently escaped notice. At the time of this writing, several United States agencies are under intense political pressure to introduce striped bass (*Morone saxatilis*) to the Great Lakes.

Perhaps the scientific turning point in documenting and analysing these kinds of change in the Great Lakes and associated inland waters came with the *Symposium on Salmonid Communities in Oligotrophic Lakes* (SCOL, Loftus and Regier 1972). The proceedings of this symposium marked the first concerted effort to describe the combined effects of exploitation, eutrophication, and species introductions on the performances of oligotrophic freshwater production systems. In addition to this triumvirate of imposed stressors, as was noted above, the effects of habitat destruction, physical modification of the catchment basin, and toxic contaminants must also be considered. The conclusions reached in the 1970s by the SCOL proceedings carry weight even now for the troubled fisheries of Atlantic Canada, especially the notion that comparative ecology can complement or even supplement many of the traditional approaches to resource management. Ideally, these methods should be reviewed and applied by the current managers of marine resources.

The status of the fisheries in Atlantic Canada

At first glance, the situation in Atlantic Canada appears quite unlike historical precedent in the Great Lakes. For example, the physical environment is far more energetic, manifesting tidal mixing and other physical forcings at scales that simply do not exist in the Great Lakes. Does this provide grounds for complacency? Of course not — recognise that this limited view merely repeats the same conventional wisdom that prevailed upon the Great Lakes four or five decades ago. The conventional wisdom now in Atlantic Canada is that anthropogenic factors cannot disrupt the integrity of Atlantic ecosystems, except in localised inshore areas. It is a familiar supposition; but it is difficult to imagine who would be so foolish as to believe it. The scale and scope of anthropogenic disturbances have increased extensively in the past five decades, and it is illogical to suppose that the factors that once disturbed the integrity of the Laurentian Great Lakes cannot exert similar impacts upon coastal marine systems, merely because they are larger in spatial extent.

More specifically, recruitment overfishing has already been experienced in Atlantic Canada, with disastrous results for the human population that has for centuries depended on those resources. We need say little more on that subject except to remark on the parallel with the postwar Great Lakes experience in the 1950s, when comparable overexploitation scenarios marked, for example, the devastation of the commercial fisheries of Lake Superior (Lawrie and Rahrer 1973), Lake Michigan (Wells and McLain 1973), and the other Great Lakes. Recruitment overfishing was the first symptom experienced in the Great Lakes, and it is therefore predictable in other systems. Indeed, similar overexploitation has already visited an ecological and human disaster on the fisheries of Atlantic Canada (Hutchings and Myers 1994). We predict there is more to come.

As noted earlier, overexploitation of the Great Lakes fisheries entailed the loss of much of the genetic structures of the salmonine and coregonine stocks that formerly contributed to the fishery. Attempts to rehabilitate the lake trout fisheries have shown that survival of the various remaining strains varies widely in different (former) spawning habitats (Burnham-Curtis et al. 1995). It is not unreasonable to suppose that similar genetic constraints may slow the recovery of the Atlantic cod (*Gadus morhua*) stocks.

Genetic fingerprinting shows that appreciable levels of genetic heteorogeneity existed among the cod stocks occupying various habitats in Atlantic Canada (Pogson et al. 1995; Ruzzante et al. 1996*a*, 1996*b*). If overfishing has shrunk the cod spawning stock biomass sufficiently to remove the barriers that formerly isolated these genotypes, as happened in the Great Lakes lake trout fishery (Burnham-Curtis et al. 1995), will cod stock recovery be similarly slowed or prevented? We have no hard data to answer that question, but on the basis of precedent in the Great Lakes, it is a plausible scenario that the cod fisheries of Atlantic Canada may not possess the genetic resources to support a speedy recovery to the configuration they had, prior to the overfishing of recent years. Recent studies in the Great Lakes demonstrate that several strains of lake trout should be used in stocking to ensure maximum use of available habitats (Elrod et al. 1996).

If the Great Lakes experience provides the precedent that we believe it does, expectations of cod stock rebuilding during the current fishing moratorium may be wildly optimistic. Instead of years or decades for stocks to rebuild, as predicted from demographic considerations, it may well require many generations before sufficient genetic diversity is reestablished in order for cod to assume their former role in the various production systems of Atlantic Canada, and of the Newfoundland fisheries in particular. Based on the Great Lakes precedent, we predict that a genetic bottleneck, caused by recent overfishing of various discrete stocks, will preclude early recovery of the various stocks of Atlantic cod to their former prominence in the fishery.

What other processes can be expected to interfere with the process of stock rebuilding? For one example, eutrophication due to anthropogenic sources is conventionally supposed to be unlikely in much of Atlantic Canada, owing to the energetic forcing resulting from tidal mixing, major currents, and comparable large-scale physical processes. These processes, one is led to believe, preclude the possibility that eutrophication could ever substantially affect the Northwest Atlantic, with the exception of localised inshore zones. Once again, this conventional wisdom is reminiscent of the same comfortable but erroneous thinking that once held the Laurentian Great Lakes to be immune from similar anthropogenic harm. The scales in the Northwest Atlantic are larger, and the processes therefore take longer to be effective, but precedent in the Great Lakes suggests that the consequences are inevitable.

Paerl (1993) has recently summarised the available information on nitrogen inputs that are transported by atmospheric deposition to coastal marine ecosystems. He estimates that 20–60% of nitrogen input to coastal waters, on a global basis, now originates from anthropogenic sources. Clearly, there is every reason to expect that the inshore waters of the global oceans are about to reflect the same pattern of eutrophication as was experienced in the Great Lakes some decades ago. Indeed, major coastal seas such as the Adriatic (Marchetti 1992; Vollenweider 1992) and Baltic (Hansson 1985; Elmgren 1989) are now severely affected by eutrophication and the initial symptoms may have become evident in the North Sea (Brockmann et al. 1988). Numerous further examples could be offered of the advent of expanding anthropogenic effects in the world's coastal seas. Certainly, there will be some delays in experiencing the inevitable in Atlantic Canada, owing to physical forcing that serves to attenuate the effects beyond the scales characteristic of the Great Lakes, but this is mere detail. The inevitable consequence will be the same. The coastal seas are poised to revisit the eutrophication experience of the Laurentian Great Lakes. Atlantic Canada will neither escape these changes nor the associated increases of toxic contaminants and habitat destruction.

It could be supposed that species introductions, at least, may constitute an exception to the Great Lakes experience. Surely, every species that could reasonably be expected to be introduced into Atlantic Canada have already been tried? There is some truth in this supposition, relative to the geologically youthful and correspondingly depauperate Great Lakes, but it ignores changed circumstances, particularly as these apply to global shipping patterns, which have changed remarkably in recent decades. Shipping now features large, fast vessels, transporting enormous volumes of ballast water on tight schedules (Carlton and Geller 1993). International traffic in ballast water effectively provides a fast, efficient method for rapidly testing the wide variety of organisms that is carried with ballast water for their abilities to colonise the changed environments provided by factors such as coastal eutrophication (Kerr and Ryder 1992). That is, the foregoing environmental changes (eutrophication, species introductions, habitat modification, etc.) do not operate independently, or in isolation from each other, but rather as an interactive set of factors that together determine the ensuing configuration and performance of the affected ecosystems.

Of the 139 species known to have been introduced into the Great Lakes, perhaps one third arrived in ballast water carried by shipping (Mills et al. 1993). The economic and ecological costs have been enormous. It should not be thought that marine coastal waters are somehow immune from this vector. Inshore communities of the west coast of the United States have undergone profound changes in their community compositions by the ballast-water vector, as have the Black and Baltic seas, and various other marine coastal locales (Carlton and Geller 1993). The Australian experience with toxic algae imported in ballast by shipping from Japan has been particularly significant to the aquaculture industry (Jones 1991). Is Atlantic Canada vulnerable to similar harmful introductions? Very probably, but there is no mechanism now in place to monitor, or prevent, entry and establishment of harmful species via this vector. The likely scenario will be a reactive program, once a harmful introduction has become established. Our primary fear is that a toxic alga may be introduced at any time, which will occasion great harm to the aquaculture industry. When that happens, inevitably in our view, the responsible management agencies will react as expected, but it will be too late. Once established, it is virtually impossible to eradicate a biological invader, as numerous prior experiences, in the Great Lakes and elsewhere, have abundantly demonstrated.

Obstacles to remedial action

Compartmentalisation is a common feature of the human analytical process, but it is antithetical to the ecosystem approach that is required in the present context. As noted earlier, the primary obstacles to remedial action that we discern are disciplinary, institutional, and jurisdictional. In turn, we now briefly consider how each of these serves to thwart analysis and action at the ecosystem level.

Disciplinary compartmentalisation of thought is a relatively recent feature of science, a product of the enormous growth of the scientific literature, especially in the current century. Attention has been increasingly drawn to this phenomenon (e.g., Rigler 1982), which is particularly a problem for the integrative sciences, such as ecology. Interdisciplinary barriers continue to constitute serious obstacles to the synthesis of an ecosystem approach to the management of our fishery resources.

Institutional barriers constitute a more formidable obstacle to the synthesis of ecological understanding. For this reason, the sizeable and very competent oceanographic community in Atlantic Canada is largely unaware of what is happening directly upstream, in the Laurentian Great Lakes. This is a direct consequence of institutional barriers to the free flow of intellectual process. It is an illogical and counterproductive approach to understanding and managing the dynamics of aquatic production systems to suppose that salinity somehow dictates a fundamental distinction, but that is the apparent reason why the Great Lakes experience is a neglected precedent in considering the future of the Atlantic Canadian fishery. Limnology and oceanography have been compartmentalised by the growth of specialised institutes and administrative divisions.

Jurisdictional barriers are the most problematic of all. There are literally hundreds of federal regulations, under the authority of numerous Acts, governing the utilisation and management of ocean-related resources. Many of these are confounded with associated provincial regulations and corresponding legislation. Management, in turn, is the responsibility of a variety of federal and provincial agencies, which in many circumstances may be unaware of overlapping concerns or even of the need to communicate on problems that are of mutual concern. It is difficult to know how to describe this complex set of problems with brevity. The approach we espouse here is to offer a concrete example, in the hope that it will illustrate some of the common problems that jurisdictional dilemmas create.

Our example concerns species introductions via ballast water carried by ships. The Australian experience was that wood-chip carriers from Japan, entering Australian waters in ballast, successfully introduced several species of toxic algae (and other unwelcome organisms) that were previously indigenous to Japanese waters. Coastal shipping subsequently spread these organisms to Australian aquaculture sites. The organisms are now irrevocably established. Risk to the Australian aquaculture industry is very serious (Jones 1991). A similar series of events will certainly occur in Atlantic Canada, as they have in the Great Lakes. It is only a matter of time and chance that will determine when they will occur, what form they will take, and how costly the consequences will be.

Our point is not to predict that such problems will occur in Atlantic Canada. Our main thesis is that consideration of how to prevent these introductions inevitably falls between the stools of the various provincial, federal, and other jurisdictions that govern or otherwise regulate the international traffic in ballast water, the fishery, and the aquaculture industry. The Australian experience shows that aquaculture and shipping are incompatible industries (Jones 1991), but a variety of agencies in Atlantic Canada is actively and independently nurturing the growth of both sectors of the economy. The basic problem is that even when the relevant agencies coexist within the same level of government, aquaculture and shipping are regarded as such disparate activities that little or no thought is given to the fact that they are in conflict, and that coordination is required. The same lack of coordination is of course amplified when jurisdiction is multiplied across a broad spectrum of federal, provincial, international, and industrial agencies, each with responsibility for some part of the overall problem.

It follows that the fish production systems of Atlantic Canada will necessarily follow the same route as was experienced in the Great Lakes, unless some means can be established to break free from the unproductive habit of compartmentalising issues to the extent that interactions are unrecognised by responsible regulatory agencies. We have offered but one example of how such oversights can occur, and that example is scarcely introduced let alone developed in full. Numerous other examples could be offered of instances where disciplinary, institutional, and particularly jurisdictional barriers prevent implementation of rational procedures for the development and management of aquatic resources in Canada.

The ecosystem approach

If the fisheries of Atlantic Canada are to escape the familiar scenario of effects that developed earlier in the Laurentian Great Lakes, the lessons of history must be put to use. We offer the following thoughts in pursuit of that desirable end.

Various statements emanating from the Canadian Department of Fisheries and Oceans (DFO) and its arms-length advisory board, the Fisheries Resource Conservation Council (FRCC), proclaim that an "ecosystem approach" to fisheries management is required in Atlantic Canada (e.g., FRCC 1995). To date, we can find no evidence of either the requisite comprehension of the concept or ensuing action in that direction, apart from some vague and essentially unsupported statements concerning possible fishery effects of seal predation and low water temperatures. If these statements accurately reflect DFO thinking on the ecosystem approach, one can be forgiven for wondering if senior and middle management of DFO understand what the term "ecosystem approach" entails. The effects of seal predation or cold water can be viewed as having ecological consequences, but recognition of their possible effects scarcely amounts to the adoption of an ecosystem approach. This is not to argue that the work of DFO and associated scientists on these questions is unimportant. Quite the contrary; the work is exemplary. Unfortunately, simple aspects of it are being extrapolated beyond reason by DFO management.

The questions remain, accordingly, "What is meant by an 'ecosystem approach', and how can it be implemented in Atlantic Canada?" Based on our joint experience, we doubt that a useful answer to either question is currently available from DFO.

Adoption of an ecosystem approach has recently been advocated in a number of different venues (e.g., Griffis and Kimball 1996; Schramm and Hubert 1996). In contrast, the same question was posed decades ago when the Canada-U.S. Joint Agreement (Great Lakes Water Quality Agreement of 1972) was first formulated for the Laurentian Great Lakes (International Joint Commission (IJC) 1978). The agreement adopted an "ecosystem approach", and its subsequent amendments (1983 and 1987) explicitly recognised that human populations, together with their various inputs, outputs, and by-products, formed an important part of the ecosystem (Vallentyne 1983). The same difficulties arose then: what is an ecosystem approach, and how is it to be implemented? The broad definition that was adopted then entailed incorporating economic, legal, and social factors, in addition to the explicitly ecological considerations that seemed obvious (Allen et al. 1993).

A tremendous amount of activity was and continues to be directed toward an ecosystem approach to the Great Lakes basin, by a wide variety of disciplinary, institutional, and jurisdictional interests. Substantial progress was made in some respects, serious mistakes made in others, and it is obvious even after decades of concerted effort that final answers have yet to be prescribed (Mehan 1996).

Implementation of an ecosystem approach to management procedures is clearly a major, dramatically new undertaking, requiring cogent input from a variety of areas of expertise. Having said that, however, we note that the interim results that have been achieved to date in the Great Lakes are quite remarkable, when the obstacles that had to be overcome are considered. That is, although the adoption of an ecosystem approach to pressing management questions may seem an intuitive and intellectually satisfying solution, its practical implementation raises complex issues (Christensen et al. 1996).

Can the Great Lakes experience be translated with profit to the implementation of an ecosystem approach to the fisheries of Atlantic Canada? We believe that there is a wealth of experience and thought, initially formulated in the Great Lakes context, that can usefully inform and guide implementation of an ecosystem approach to the Atlantic fisheries. The proceedings of the SCOL, noted earlier, described some of the commonalities in the responses of aquatic ecosystems to imposed stress. There are significant differences between the Great Lakes and Atlantic ecosystems, but there are many fundamental similarities in the ecological, political, social, legal, and economic senses. Our belief is that these common properties can be studied with profit, and that we can learn from experience, but only if all relevant parties are adequately consulted.

Experience with the Great lakes situation has proven that a wide variety of parties must necessarily be involved. The Great Lakes fisheries management agencies alone were not sufficient to the task. In fact, the primary control exerted by the fisheries agencies proved to be one of the initial obstacles to evolving an ecosystem approach, because the objectives of major players in the fishery differed substantially in many instances from the objectives of other interests. This is quite apart from the additional problem that the various state, provincial, and federal fisheries agencies often pursued conflicting management objectives within a single ecosystem. Obviously enough, fisheries management agencies espouse some primary objectives and priorities that are quite different than would be put forward, for example, by conservation agencies, human health authorities, native peoples, municipalities, or various industrial or public interest groups, to name just some of the potentially affected parties. It also follows that the university sector in particular must play an increasingly prominent role in this policy revolution, because only that source can offer the breadth of disciplinary expertise that is required for the task.

The current approach in the Great Lakes context involves participation by many agencies, including various international, federal, state, and provincial sectors, together with a large and valuable input from the public sector, including universities, native peoples, municipalities, and various industrial components. Quite obviously, it will be difficult if not impossible for DFO to freely relinquish its sole control over Atlantic Canadian fisheries by accommodating other inputs, regardless of how necessary these may be to achieving a sound solution to existing and impending problems. This situation is only natural, because DFO authority on the east coast is absolute, and lacks even the source of moral persuasion that an IJC or Great Lakes Fishery Commission (GLFC) is able to exert in the Great Lakes context. It is a rare phenomenon indeed for a federal bureaucracy to admit it is unequal to the task at hand, and ask for help.

The remaining question is how this revolutionary change of policy, to accommodate an ecosystem approach, can be initiated in Atlantic Canada. There should be no mistake that the call for an ecosystem approach to the Atlantic fisheries requires a fundamental change of thought, just as it did in the Great Lakes ecosystem. It raises the question as to whether the existing institutional and jurisdictional venues that affect the fishery are capable of recognising the need for change, and responding accordingly, or whether they will mistakenly interpret the call for ecosystem management as just a different caption for conducting business as usual. It will be vitally important to determine whether the existing management system can adapt to the challenge, or whether it must be replaced before meaningful change can occur.

It is particularly relevant to contrast the management regimes that have developed in the Great Lakes and Atlantic Canada. While few would argue that the current system is perfect (Dochoda and Koonce 1994), the Great Lakes experience has, after decades of experimentation, come to be founded upon the collective experience and judgement of numerous affected parties. In general, these now agree that consensus is the appropriate mode of action. This may seem to constitute a small gain, but recognise that it took decades to accomplish. Contrast this realisation with the exclusive regime that currently obtains in Atlantic Canada, where DFO effectively exerts sole control over the fishery, and by association, over the entire ecosystem. This situation is reminiscent of the Great Lakes situation in the 1950s and 1960s, when fisheries management was the prerogative of fisheries agencies, to the detriment of effective ecosystem management.

Current and impending changes in Atlantic Canada

For several reasons, the current situation in Atlantic Canada is fluid and difficult to predict. Establishment in 1993 of the FRCC has potentially provided the Minister of DFO with an independent source of advice. Optimistically, this agency could grow to embrace the same breadth of ecosystem interests as has characterised the influence exerted in the Great Lakes ecosystem by the GLFC and the IJC. If so, this could augur well for the future. Since its inception, however, the FRCC has been mired in its initial challenge of brokering the remaining fisheries resources among the traditional claimants. Whether it can move beyond this initial imperative remains to be seen. We see no evidence that it possesses either the motivation or will to do so.

Our current perception is that the FRCC is too much the handmaiden of DFO and the traditional fisheries interests to be able to adopt the broadly defined ecosystem perspective that was espoused by the GLFC and the IJC in the Great Lakes context. If so, the FRCC is destined to be ineffective in the larger sense of an ecosystem context, and will be bypassed as events overtake it. All things considered, it took decades of contention among the various Great Lakes agencies before agreement upon consensus management was reached; it is doubtless too much to expect that similar accommodation can be reached in Atlantic Canada in the absence of meaningful contributions by all affected parties, many of whom apparently do not yet realise they should be involved.

A second consideration, perhaps a hopeful development, is the apparent realisation by the members of fishers' organisations that they can no longer survive as individual entrepreneurs, and must therefore band together in self-defence. For one example, among several possibilities, the Scotia–Fundy Fixed Gear Groundfish Committee, an association of inshore operators and processors, has come together to formulate their own proposals for conservation harvesting plans. To those versed in the individualism characteristic of successful fishers, this is a remarkable development and it is astonishing to observe the rapidity and acumen with which they have mastered the essentials of the challenge. In the short time available to them, they have comprehended the need to move to a community-based management perspective transcending individualism, and have shown lively understanding of an ecosystem approach to resource management. It remains to be seen whether associations such as this can withstand the influence exerted by the major corporations, who enjoy ready access to the virtually dictatorial powers of DFO over the fish production systems of Atlantic Canada.

A further uncertainty, unclear and unresolved at the time of this writing, is what will be contained in Canada's long-promised "Oceans Act" and "Fisheries Act". It may well be that the federal cabinet has been provided with sound advice, and the legislation will propose accordingly. Of course, it is also possible that federal bureaucrats will have failed to understand what is happening, not for the first time, and cabinet will be shown to have acted on unsound advice. Time will tell, but on the basis of the Great Lakes experience, the window of opportunity to set the Atlantic Canadian fisheries on a provident course is rapidly closing, and unless appropriate action is taken, soon much will be lost, irrevocably.

Perhaps the very root of the problem in Atlantic Canada is that it is perceived solely as a fisheries conundrum. That is, if only the exploitable stocks can somehow be rebuilt, then all will be well. This is wishful thinking that flies in the face of experience. The Great Lakes experience taught us that ecosystem debilitation is a complex amalgam of interacting causal factors; to assume otherwise in Atlantic Canada and hope for speedy recovery of seriously overfished spawning stock biomass amounts to spitting against the wind.

It is therefore unfortunate that the problems visited upon the Atlantic fisheries have come to be perceived solely as fisheries recruitment insufficiencies. For that reason, as devastatingly unfortunate as that may be, the larger context of the problem is at risk of being overlooked. The fact is, based on the Great Lakes experience, the entire ecosystem is at risk.

Taken together, there is ample reason to fear for the future of Atlantic Canada's fish production systems. There is abundant precedent from the Great Lakes experience to show that a taxing series of impacts is unfolding in Atlantic Canada. It is also clear that the existing regulatory agencies are decades behind the Great Lakes agencies in acquiring the competence and institutional capacities to deal with the current and impending problems. We have serious reasons to doubt that the existing regulatory regime is, or will be, equal to the task required.

In our view, it is essential to implement an ecosystem management approach to Canada's Atlantic aquatic resources. Based on the Great Lakes experience, this can only succeed under the rubric of a new institutional framework that involves all affected parties. The requisite framework must necessarily be immune from direct political intervention; thus, no single government department should be entrusted with the responsibility. We do not know what the best framework is; this is something best left to all those affected to determine. We do know, however, that the GLFC and the IJC, despite their limitations, have been very effective in helping to orchestrate an ecosystem approach to the Great Lakes. It follows that something like this model should be considered when considering the new order. Certainly, judging by recent events in the Atlantic fisheries, we have nothing to lose by trying.

References

Allen, T.F.H., Bandurski, B.L., and King A.W. 1993. The ecosystem approach: theory and ecosystem integrity. Report to the Great Lakes Science Advisory Board. International Joint Commission, United States and Canada (Washington, D.C., Ottawa, Ont., Windsor, Ont.).

Brockmann, U., Billen, G., and Gieskes, W.W.C. 1988. North Sea nutrients and eutrophication. *In* Pollution of the North Sea. *Edited by* W. Salomons, B.L.Bayne, E.K. Duursma, and U. Forstner. Springer-Verlag, Berlin. pp. 370–389.

Burnham-Curtis, M.K., Krueger, C.C., Schreiner, D.R., Johnson, J.E., Stewart, T.J., Horrall, R.M., MacCallum, W., Kenyon, R., and Lange, R.E. 1995. Genetic strategies for lake trout rehabilitation: a synthesis. J. Gt. Lakes Res. **21**(Suppl. 1): 477–486.

Carlton, J.T., and Geller, J.B. 1993. Ecological roulette: the global transport of nonindigenous marine organisms. Science (Washington, D.C.), **261**: 78–82.

Carr, J.F. 1962. Dissolved oxygen in Lake Erie, past and present. Gt. Lakes Res. Div. Inst. Sci. Technol. Univ. Mich. Publ. No. 9. pp. 1–14.

Christensen, N.L. (*Chair*), Bartuska, A., Brown, J.H., Carpenter, S., D'Antonio, C., Francis, R., Franklin, J., MacMahon, J., Noss, R., Parsons, D., Peterson, C., Turner, M., and Woodmansee, R. 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. Ecol. Appl. **6**: 665–691.

DeVault, D.S., and Weishaar, J.A. 1983. Contaminant analysis of 1981 fall run coho salmon (*Oncorhynchus kisutch*). USEPA, Great Lakes National Program Office, Chicago, Ill. EPA-905/3-83-001.

DeVault, D.S., and Weishaar, J.A. 1989. Contaminant analysis of 1992 fall run coho salmon (*Oncorhynchus kisutch*). USEPA, Great Lakes National Program Office, Chicago, Ill. EPA-905/3-84-004.

Dochoda, M.R., and Koonce, J.F. 1994. A perspective on progress and challenges under a joint strategic plan for management of Great Lakes fisheries. Univ. Toledo Law Rev. **25**: 425–441.

Elmgren, R. 1989. Man's impact on the ecosystem of the Baltic Sea energy flows today and at the turn of the century. Ambio, **18**: 326–332.

Elrod, J.H., O'Gorman, R., and Schneider, C.P. 1996. Bathythermal distribution, maturity, and growth of lake trout strains stocked in U.S. waters of Lake Ontario, 1978–1993. J. Gt. Lakes Res. **22**: 722–743.

Francis,G.R., Magnuson, J., Regier, H., and Talhelm D. 1979. Rehabilitating Great Lakes ecosystems. Gt. Lakes Fish. Comm. Tech. Rep. No. 37.

FRCC. 1995. 1996 conservation requirements for Atlantic groundfish. FRCC.95.R.2. Fisheries Resource Conservation Council, Ottawa, Ont.

Griffis, R.B., and Kimball, K.W. 1996. Ecosystem approaches to coastal and ocean stewardship. Ecol. Appl. **6**: 708–712.

Hansson, S. 1985. Effects of eutrophication on fish communities with special reference to the Baltic Sea — a literature review. Inst. Freshwater Res. Drottningholm Rep. **62**: 36–56.

Hutchings, J.A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Can. J. Fish. Aquat. Sci. **53**: 943–962.

Hutchings, J.A,. and Myers, R.A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Can. J. Fish. Aquat. Sci. **51**: 2126–2146.

IJC. 1978. Great Lakes Water Quality Agreement of 1978. Ammended 1983, 1987. International Joint Commission, Washington, D.C., Ottawa, Ont., Windsor, Ont. (Reprinted 1994.)

Jones, M.M. 1991. Marine organisms transported in ballast water: a review of the Australian scientific position. Bur. Rural Resour. Bull. No. 11. Australian Government Publishing Service, Canberra.

Kerr, S.R., and Ryder, R.A. 1992. Effects of cultural eutrophication on coastal marine fisheries: a comparative approach. Sci. Total Environ. Suppl. **1992**: 599–614.

Lawrie, A.H., and Rahrer, J.F. 1973. Lake Superior — a case history of the lake and its fisheries. Gt. Lakes Fish. Comm. Tech. Rep. No. 19.

Loftus, K.H., and Regier, H.A. (*Editors*). 1972. Proceedings of the Symposium on Salmonid Communities in Oligotrophic Lakes. J. Fish. Res. Bd. Can. **29**: 611–986.

MacKenzie, D. 1995. The cod that disappeared. New Scientist. 16 Sept.

Marchetti, R. 1992. The problems of the Emilia–Romagna coastal waters: facts and interpretations. Sci. Total Environ. Suppl. **1992**: 21–33.

Mehan, G.T. 1996. Ecosystem management in the Great Lakes basin. Fisheries, **21**: 12–13.

Mills, E.L., Leach, J.H., Carlton, J.T., and Secor, C.L. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. J. Gt. Lakes Res. **19**: 1–54.

Paerl, H.W. 1993. Emerging role of atmospheric nitogen deposition in coastal eutrophication: biogechemical and trophic perspectives. Can. J. Fish. Aquat. Sci. **50**: 2254–2269.

Parsons, J.W. 1967. Contributions of year-classes of blue pike to the commercial fishery of Lake Erie, 1943–59. J. Fish. Res. Board Can. **24**: 1035–1066.

Pogson, G.H., Mesa, K.A., and Boutilier, R.G. 1995. Genetic population structure and gene flow in the Atlantic cod *Gadus morhua*: a comparison of allozyme and RFLP loci. Genetics, **139**: 375–385.

Regier, H.A., Applegate, V.C., and Ryder R.A. 1969. The ecology and management of the walleye in western Lake Erie. Gt. Lakes Fish. Comm. Tech. Rep. No. 15.

Rigler, F.H. 1982. The relation between fisheries management and limnology. Trans. Am. Fish. Soc. **111**: 121–132.

Ruzzante, D.E., Taggart, C.T., Cook, D., and Goddard, S. 1996*a*. Genetic differentiation between inshore and offshore Atlantic cod (*Gadus morhua*) off Newfoundland: microsatellite DNA variation and antifreeze level. Can. J. Fish. Aquat. Sci. **53**: 634–645.

Ruzzante, D.E., Taggart, C.T., and Cook, D. 1996*b*. Spatial and temporal variation in the genetic composition of a larval cod (*Gadus morhua*) aggregation: cohort contribution and genetic stability. Can. J. Fish. Aquat. Sci. **53**: 2695–2705.

Schramm, H.L., and Hubert, W.A. 1996. Ecosystem management: implications for fisheries management. Fisheries, **21**: 6–11.

Sly, P.G. 1991. The effects of land use and cultural development on the Lake Ontario ecosystem since 1750. Hydrobiologia, **213**: 1–75.

Smith, S.H. 1962. Lake Erie or Lake Eerie? Izaak Walton Mag. 1962. pp. 4–5.

Smith, S.H. 1972. Destruction of the ecosystem in the Great Lakes and possibilities for its reconstruction. Progress in fishery and food science. Univ. Wash. Publ. Fish. New Ser. Vol. 5.

Vallentyne, J.R. 1974. The algal bowl: lakes and man. Dep. Environ. Can. Misc. Spec. Publ. No. 22.

Vallentyne, J.R. 1983. Implementing an ecosystem approach to management of the Great Lakes basin. Environ. Conserv. **10**: 273–274.

Vollenweider, R.A. 1992. Coastal marine eutrophication: principles and control. Sci. Total Environ. Suppl. **1992**: 1–20.

Wells, L., and McLain, A.L. 1973. Lake Michigan — man's effects on native fish stocks and other biota. Gt. Lakes Fish. Comm. Tech. Rep. No. 20.

Is scientific inquiry incompatible with government information control?

Jeffrey A. Hutchings, Carl Walters, and Richard L. Haedrich

Abstract: Government-administered science in Canada, and its potential for bureaucratic and political interference, merits examination in the wake of the biological and socioeconomic catastrophes associated with recent fishery collapses. We cite specific research on Atlantic cod (*Gadus morhua*) and Pacific salmon (*Oncorhynchus* spp.) habitat to illustrate how nonscience influences can interfere with the dissemination of scientific information and the conduct of science in the Canadian Department of Fisheries and Oceans. The present framework for linking fisheries science with fisheries management has permitted, intentionally or unintentionally, a suppression of scientific uncertainty and a failure to document comprehensively legitimate differences in scientific opinion. We suggest that the conservation of natural resources is not facilitated by science integrated within a political body. The formation of a politically independent organization of fisheries scientists, or some such reorganization of the link between scientific research and the management of natural resources, merits serious and open debate.

Résumé : La science administrée par le gouvernement au Canada, et sa vulnérabilité à l'intervention bureaucratique et politique, doit faire l'objet d'un examen à la suite des catastrophes biologiques et socio-économiques liées à l'effondrement récent des pêches. Nous citons de la recherche spécifique sur la morue franche (*Gadus morhua*) ainsi que l'habitat du saumon du Pacifique (*Oncorhynchus* spp.) pour démontrer comment des interventions non scientifiques peuvent gêner la diffusion de l'information scientifique et la conduite de la science au ministère des Pêches et des Océans du Canada. Le cadre de travail actuel de liaison entre les sciences halieutiques et la gestion des pêches a permis, intentionnellement ou non, que l'on fasse fi de l'incertitude scientifique et que l'on néglige de documenter de manière complète et détaillée les différences d'opinion scientifique légitimes. Nous estimons que la conservation des ressources naturelles n'est pas facilitée par l'intégration de la science dans un organisme politique. La création d'un organisme politiquement indépendant de scientifiques des pêches ou une quelconque réorganisation en ce sens du lien entre la recherche scientifique et la gestion des ressources naturelles devrait faire l'objet d'un débat sérieux et ouvert.
[Traduit par la Rédaction]

Introduction

Integration of fisheries science within government is a relatively recent phenomenon in Canada. Prior to 1972, most research had been conducted under the auspices of the politically independent Fisheries Research Board of Canada (FRB). The FRB was dissolved in 1979 with the creation of the Department of Fisheries and Oceans (DFO), within which the full integration of fisheries science within a political body was complete.

Concomitant with the creation of the DFO were two events whose unfolding would later result in intense public scrutiny of the Department. One of these was the extension of Canada's fisheries jurisdiction to 200 miles in 1977. This effectively placed the responsibility for managing eastern Canada's groundfish fisheries with the federal government. Fourteen years later, commercial exploitation of Newfoundland's northern cod, *Gadus morhua*, ended because of a nearly 100-fold reduction in spawner biomass of what once was the largest cod fishery in the world (McGrath 1911). The second event occurred on the Pacific coast. This was the reduction in water flows of British Columbia's Nechako River, a large tributary of the Fraser River, effected by the Aluminum Company of Canada (ALCAN) in the late 1970s. Concern for the negative effects that reduced flows might have on salmon productivity prompted legal actions against ALCAN by the DFO in the early and mid-1980s before a much-criticized (British Columbia Utilites Commission (BCUC) 1994) out-of-court settlement on flow regimes was reached in 1987.

Recent declines in Atlantic cod (Hutchings and Myers 1994) and Pacific salmon, *Oncorhynchus* spp. (Walters 1995), coupled with clearly negative socioeconomic consequences, warrant examination of the means by which fisheries science is conducted, interpreted, and publicly presented by the DFO. Following a brief overview of the distinction between fisheries science and fisheries management, we cite specific examples of bureaucratic influence on government science related to northern cod and to the Nechako River settlement. Regarding Atlantic cod, we document nonscientific influences on the dissemination of information pertaining to its biology, ecology, and abundance that have deleteriously affected strategies designed to sustain the stocks in the past, have hindered scientific efforts to understand fully the causes of the present collapses, and, without change, are likely to limit the effectiveness of strategies to prevent fishery collapses in the future. Failure to document and (or) failure to acknowledge fully scientific uncertainty and variability in scientific opinion on the status of cod stocks were features common to the attainment of the Nechako Settlement Agreement. We contend that political and bureaucratic interference in government fisheries science

Received July 2, 1996. Accepted February 27, 1997.
J13525

J.A. Hutchings. Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada.
C. Walters. Fisheries Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.
R.L. Haedrich. Department of Biology, Memorial University of Newfoundland, St. John's, NF A1B 3X9, Canada.

Can. J. Fish. Aquat. Sci. **54**: 1198–1210 (1997)

compromises the DFO's efforts to sustain fish stocks and, thereby, the socioeconomic well-being of fishing people and fishing communities. There is an urgent need for public scrutiny of the influence of senior-level bureaucrats in the management of Canada's natural resources.

There is much variability in fisheries science and in stock assessment documents within and among the different regional branches of the DFO. Thus, our comments and criticisms of the dissemination of the results of fisheries research may not be wholly applicable to all regions and (or) to the stock and habitat assessments of all species. We also want to be very clear that our criticisms are directed at the present *system* of government-administered science and its facilitation of bureaucratic/political interference, *not* at individuals.

Communication between fisheries science and fisheries management

Fisheries science conducted within the DFO is an exercise distinct from fisheries management. Fisheries science develops information on the biology and population dynamics of exploited fishes, upon which rational management can be based. Such information can include data on age structure, movement and migration, vertical and horizontal patterns of abundance (i.e., distribution), interrelationships with other species, morphological, behavioural, and genetic distinctiveness, life history strategies, and associations between physical environmental factors (e.g., temperature, water flow, salinity) and biological variables (e.g., growth rate, survival). Fisheries science is the responsibility and primary activity of a professional cadre of research scientists. As in any branch of science, there are uncertainties and different interpretations associated with the quality of fisheries data, analysis, and interpretation. This situation leads to the formulation and testing, and reformulation and retesting, of alternative hypotheses to explain processes, patterns, and variability. This is a good thing; this is how science works. For commercially exploited fishes, particularly important hypotheses and debates are about interannual variability in recruitment, spatial and temporal differences in fish location, and spatiotemporal changes in fish mortality and stock structure.

Fisheries management consists of establishing and implementing regulations intended to maintain fish abundance at or above conservation targets. To control fishing mortality, these regulations can take the form of catch quotas (e.g., Total Allowable Catches (TACs), Individual Transferable Quotas), effort restrictions (e.g., minimum mesh sizes, maximum vessel sizes, season limits), and other measures to limit exploitation rates directly. Indirect protection of fish occurs through regulations that identify limits to which fish habitat can be manipulated (e.g., establishment of minimum water flow regimes, limitation of stream channelization, elimination of the influx of chemical pollutants).

Uncertainties in data and the existence of alternative hypotheses are often not evident in the science documents upon which management bases (in consultation with industry) its decisions. For example, rather than including confidence intervals on abundance metrics or demonstrating how one's perception of stock abundance is dependent on the validity of different sets of assumptions, stock assessment documents have often provided only a single perception of the health of a stock, and little or no indication either of the variability associated with the various parameters used in abundance models or of the robustness of these models to such variability (e.g., Baird et al. 1992).

It is also important to note that science documents have not been developed in close linkage with analyses of policy options. Hence, they do not contain direct assessments of the various options identified by managers and industry. The discordance is intentional, as noted by a former DFO Assistant Deputy Minister for Science: "It is the role of the Minister and not of public servants to make policy decisions affecting the fishery" (Morrissey 1993, p. 4). This direct consequence of the Act that established the DFO has led to the assumption that science can be used in policy assessment without the necessity of having scientific questions stated explicitly in terms of precise and particular policy alternatives.

Collapse of Atlantic cod in eastern Canada

Assessment of stock status

Assessment documents on Atlantic groundfish stocks seldom reflect the full range of opinions that often exist among scientists regarding the "health" of fish stocks. Although dissenting opinions can be expressed at stock assessment meetings, it is the "scientific consensus" on things such as present and past levels of fishing mortality and stock biomass that is paramount in the final stock assessment document. An example is presented below. By not acknowledging formally the existence of differing opinions on the health of a fish stock, and by not reporting and quantifying sources of variability and their effects on the robustness of abundance models, the transfer of scientific information to fishery managers bears little resemblance to the means by which scientific information is communicated, debated, and accepted by scientists in general.

Prior to 1993, scientific advice on eastern Canadian groundfish stocks was provided by the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC). Every year, data and stock assessment analyses pertaining to commercially exploited fishes were presented as CAFSAC Working Papers by DFO scientists to other DFO scientists in CAFSAC Subcommittees (e.g., the CAFSAC Groundfish Subcommittee dealt with Atlantic cod stock assessments). Working Papers accepted as CAFSAC Research Documents provided the supporting documentation and analysis for stock assessment. Subcommittee reports summarizing stock status, detailing specific advice, and recommending additional research constituted the primary source of information for the CAFSAC Steering Committee. Subcommittee reports were not available to the public. Following its vetting of these reports, the Steering Committee prepared Advisory Documents which formed the primary source of scientific information for the Atlantic Groundfish Advisory Committee (AGAC), the committee of industry and government (federal and provincial) representatives that provided recommendations to the senior managers and planners within the management structure of the DFO.

In principal, the flow of scientific information through these committees and subcommittees, from "raw" data to consensual interpretation, has a certain logic. It is clear why such a process is appealing to bureaucratic institutions whose leadership requires that "specialist" information (e.g., scientific data and interpretation) be pared down to simple essentials before it can be used in reaching management decisions. But there clearly are risks associated with paring away too much information. For example, in 1990, CAFSAC (1990) identified three exploitation options for the 1991 TAC for northern cod: (*i*) 100 000 t, the TAC corresponding to the conservation-based $F_{0.1}$ target fishing mortality of $F = 0.20$ (under the $F_{0.1}$ strategy, the target instantaneous rate of fishing mortality, F, corresponds to the point on the dome-shaped relationship between yield per recruit and F at which the slope is 10% the slope at the origin; at $F = 0.20$, 18% of the harvestable biomass is removed by fishing), (*ii*) 150 000 t, the TAC corresponding to the "50 percent" rule, i.e., set next year's TAC halfway between the TAC corresponding to $F_{0.1}$ and this year's TAC, and (*iii*) 170 000 t, the TAC corresponding to $F = 0.40$, i.e., double the $F_{0.1}$ fishing mortality. However, CAFSAC (1990, p. 114) advised that there was no need to reduce fishing mortality to the $F_{0.1}$ target in 1991. Because of this recommendation, the $F_{0.1}$ TAC was not considered by AGAC (AGAC 1990). Rather, the exploitation options for 1991 debated by AGAC were 150 000, 170 000, and 200 000 t (i.e., status quo). These management options were presented to AGAC with little information as to the probability that the stock would grow under each option or the risk that each option posed in regard to the sustainability of the stock (CAFSAC 1990). The Minister of Fisheries and Oceans subsequently set the 1991 TAC at 190 000 t. The moratorium on the collapsed northern cod stock was announced the following year.

The primary objectives of those involved in stock assessment are to determine the range of possible states of nature and to evaluate the consequences of alternative management actions; the job of fishery managers is to choose the management action. Failure to transmit scientific uncertainty to decision makers, and an apparent inability and (or) unwillingness of decision makers to acknowledge uncertainty and to make decisions in the face of it, has been discussed in detail by Hilborn et al. (1993).

Scientific concerns regarding stock status of northern cod in 1986

One example of how difficult it has been for government to deal with scientific uncertainty is the means by which concerns regarding the legitimacy of the June 1986 Stock Assessment of northern cod were addressed. In October 1986, a meeting was called at the DFO, Newfoundland Region (St. John's), to consider reasons for the apparent discrepancy in the availability of cod to the inshore and offshore fisheries (the inshore fishing sector had been arguing that their catches were low because of overexploitation by offshore trawlers) and to address uncertainties associated with the most recent abundance estimates of northern cod. A list of questions was compiled and forwarded to CAFSAC: these questions were addressed at a meeting on 14 November 1986.

Among the CAFSAC Working Papers presented at the November meeting was one authored by Dr. George Winters (Head of the Pelagic Fish, Shellfish, and Marine Mammals Division, Newfoundland Region) entitled "Aide-memoire on 2J3KL assessment: *non gratum anus rodentum*?" Winters' main conclusions were that the size of the cod stock had been overestimated since 1977 (leading to the result that fishing mortalities were in excess of those reported in the 1986 stock assessment) and that this overestimation was caused by excessive reliance on abundance indices derived from commercial trawler catch rate data and by violation of assumptions of the multiplicative model used in the assessment procedure. Winters' unpublished paper is important because it represents one of the few in which disagreements based on assessment methodology related to northern cod stock assessments are documented. The manner with which the DFO dealt with the concerns expressed by Winters, and by non-DFO scientists (e.g., Keats et al. 1986), concerning the health of the northern cod stock serves as an excellent example of the potential incompatibility of government bureaucracy and normal scientific inquiry.

To sum the main points of Winters' short document (Winters 1986, pp. 1–2, italics added):

> "The impetus for my effort arises out of the uneasiness which I experience when I peruse the STACFIS [Standing Committee on Fishery Science] report on 2J3KL [northern] cod. Not only is its train of thought inconsistent but quite often there are no passengers on it. For example, it concludes that, while trends in commercial catch rates may be good indicators of stock abundance, the magnitude of such changes with time may not be reliable, due, in part, to violations in certain assumptions of the data treatment model (the Gavaris Multiplicative Model). It further concludes that the results of cohort analyses using [autumn research] survey data should also be viewed with caution because of environmental effects, *yet no analysis was performed to show that such effects were present in the data available.* Both indices were, however, used to estimate F_T [terminal fishing mortality] with widely divergent conclusions as to stock status and STACFIS assumed that the true status was at some intermediate (and arbitrary) point. There was no rigorous consideration of the two other alternatives that (*i*) estimates of F_T by the Commercial C/R [catch rate] and the survey index were biassed in the same direction or that (*ii*) only one abundance proxy was biassed and that its estimate of F_T should be discarded unless the direction and magnitude of such a bias could be evaluated."

Winters' analysis went on to address these biases and to document the strong influence that a given abundance metric can have on estimates of fishing mortality. Winters also examined briefly possible reasons for the recent failures in the inshore fishery. Contrary to the consensus expressed by Lear et al. (1986) that had concluded that cold water temperatures were responsible for low inshore catches in 1985, Winters documented a statistically significant negative association between inshore catch and offshore exploitation rate, concluding that (Winters 1986, p. 8) "the decline in the inshore catches since 1982 has been due to the increase in the offshore exploitation rate" (Winters 1986, pp. 8–9):

> "There is sufficient evidence to suggest that the assessment of 2J3KL Cod agreed upon by STACFIS in June 1986 presents an overestimate of stock abundance and this bias has been a consistent pattern at least as far back as the late 1970's. This error appears to be largely a result of a heavy dependence on commercial catch-rates as the major calibration source for cohort analysis and the biases introduced into such catch-rates by the violations in the assumptions of the Multiplicative Model used to standardize such data. Given this conclusion and considering the results from the

> Canadian surveys, the recent failures in the inshore fishery can be explained by accrued over-fishing of this stock as a result of persistently inappropriate advice on TAC levels."

CAFSAC's response and research recommendations

The first two questions posed to CAFSAC in October 1986 appear to address Winters' concerns (CAFSAC 1986): Question 1: "What is the current [1986] status of the Div. 2J3KL cod stock (4+ biomass and spawning biomass) in relation to its size in 1977?" Question 2: "What have catches been since 1977 (including estimated foreign activity) in relation to the $F_{0.1}$ objective?"

CAFSAC's response to Question 1 is peculiar. It begins by detailing uncertainties associated with abundance data estimated from research surveys and commercial trawler catch rates. After noting that the survey and commercial catch rate data gave divergent trends in abundance (the latter showing an increase in abundance since 1983, the former showing a decline), and that a revised weighting procedure produced a trend consistent with that based on the survey data, CAFSAC agreed with Winters (1986) that "these differences in the indices of stock abundance indicate...uncertainty with respect to the current estimates of stock size" (CAFSAC 1986, p. 4). However, CAFSAC went on to state that "the level of uncertainty in these estimates is not unusual in comparison with the assessment of other cod stocks in the Northwest Atlantic" (CAFSAC 1986, p. 4). This odd and clearly unscientific means of addressing acknowledged uncertainties in stock abundance is followed by implicit dismissal as CAFSAC concluded its response to Question 1 by restating the increases in stock abundance between 1977 and 1987 predicted by the June 1986 Stock Assessment.

CAFSAC's response to Question 2 included the statement that "annual population sizes since 1977 have been overestimated in previous assessments....$F_{0.1}$ catches based on the revised estimates of annual population size are considerably lower [30% to 70% lower; Fig. 8 in CAFSAC 1986] than the $F_{0.1}$ catches actually advised." Thus, it was recognized that the abundance of northern cod from 1977 to 1985 was probably considerably less than had been previously believed and that fishing mortalities had been approximately double the intended, and presumed sustainable, target levels.

Others were also questioning the stock status of northern cod in 1986 (see Steele et al. 1992). CAFSAC's conclusions regarding (*i*) uncertainties associated with abundance estimates, (*ii*) overestimation of stock abundance, and (*iii*) underestimation of fishing mortality were also reached by the authors of the first independent, albeit industry-sponsored, review of northern cod assessments (Keats et al. 1986). Researchers at Memorial University of Newfoundland concluded that (Keats et al. 1986, p. 23)

> "There is no evidence that the stock has continued to increase since 1981–82. Problems with catch rate and survey abundance indices suggest that we have no real idea of what is the true value of F_t [i.e., F_T], and therefore no idea of the true pattern of biomass change in recent years. Catch rate indices contain an unknown degree of bias. Survey abundance indices suggest a decrease in abundance of fully recruited cod in 2J+3K since 1981–82. Inshore landings have gone down since 1982. Unfortunately, as with offshore catch rates, which tell us very little, we also have no measure of inshore effort. Gill net landings have declined dramatically. Cod trap landings have not gone up since 1977. Where are the fish? Offshore? Where is the evidence? These observations suggest that the fishery has not continued to recover from the influence of foreign overfishing offshore, and that the northern cod in 3KL is currently being fished at a rate much higher than that which would allow the stock to increase. At the very least, this suggestion should be given much more serious consideration than it evidently has been given by NAFO [Northwest Atlantic Fishery Organisation], CAFSAC and AGAC."

The main conclusion of this review was that cod abundance was significantly lower than indicated by DFO assessments because of consistent underestimation of F, the same view expressed by CAFSAC (1986). The chair of CAFSAC's Steering Committee from 1989 to 1993 observed that the Keats et al. (1986) review was "not taken very seriously...by DFO Science [in 1986]...because the analysis was somewhat naive. It was easy for us to discount it" (see Finlayson 1994, p. 48). Based on interviews with DFO scientists and nonscience DFO employees, Finlayson (1994, p. 38) concluded:

> "The response from DFO was to dismiss the Keats Report as superficial. It was researched and written in only four weeks and, DFO claimed, axiomatically biased, pseudoscience written to support the political agenda of the Newfoundland Inshore Fisheries Association [who sponsored the review]."

The scientific validity of these responses to the review by Keats et al. (1986) must be assessed in light of the observation that CAFSAC had reached the same conclusions as the independent review at about the same time and using the same data. Furthermore, many of the concerns expressed by Keats et al. (1986) regarding the lack of data on the effects of fishing on cod (e.g., data on effort, size- and age-selectivity of gear) were also identified by CAFSAC in the recommendations that comprised their response to Question 18 which asked, "What specific research can be undertaken before the June 1987 assessment to better allow precise answers to questions of the type posed above?" In addition to physical and biological oceanographic analyses, CAFSAC suggested that studies be undertaken to (*i*) quantify effort and catch rates in the inshore and offshore fisheries, (*ii*) assess the validity of the assumptions of the multiplicative model (*iii*) identify potential biases in the research survey data, (*iv*) quantify discarding rates and include them in the assessment process, and (*v*) determine the fishing selectivity of each major gear type. CAFSAC's 1986 recommendations that had yet to be addressed by 1995 included (*i*) a comprehensive analysis of the spatial structure of cod as reflected by survey data, (*ii*) the documentation of and errors associated with catch discards from all gear types and an evaluation of the effects of discarding on abundance estimates, and (*iii*) the determination of age- and size-specific vulnerabilities of cod to different fishing gear.

Failure to enact CAFSAC's recommendations

Why were the most important of CAFSAC's recommendations — those dealing with the effects of fishing — not enacted by the DFO prior to the June 1987 assessment? Why did the DFO not publicly acknowledge that the concerns raised by Keats et al. (1986) were the same as those that had been identified by CAFSAC and that recommendations had been formulated to address them? CAFSAC's Advisory Document would have lent credence to the arguments of those who had identified sources of uncertainty in the means by which the stock status of northern cod was being assessed and had argued that the abundance of northern cod was less than the estimates being provided by the DFO.

One factor that may have loomed large in a failure to act was the extremely high abundance of northern cod estimated from the research surveys conducted during the autumn of 1986. This anomalously high estimate had the effect of bringing the survey abundance estimates in agreement with those estimated from the commercial trawler catch rate data (see Baird et al. 1991; Hilborn and Walters 1992). The illusion that the stock was in terrific shape may have led DFO officials to conclude that there was no immediate need to investigate the questions posed by CAFSAC. But, rather than treating the 1986 survey-based estimate with the scientific suspicion it deserved (given the abundance data of previous surveys, it was impossible for the stock to have grown so much in a single year), the estimate was included in the 1987 assessment (Baird and Bishop 1987). This may explain why the DFO did not act upon CAFSAC's recommendations and why it publicly criticized the conclusions of Keats et al. (1986). For, if the 1986 survey abundance was even close to being accurate, the stock was not in the midst of decline, as suggested by Winters (1986) and by Keats et al. (1986), but was growing as argued in the 1986 stock assessment (Baird and Bishop 1986).

Would the uncertainties regarding the status of northern cod in 1986 have been summarily dismissed by a scientific establishment with no political or governmental affiliation? It is difficult to imagine that scientists concerned with the status of northern cod would not have persisted in their efforts to quantify these uncertainties and to evaluate their influence on stock abundance and corresponding TACs (e.g., a group of independent scientists who reviewed the northern cod stock assessments in 1987 concluded that the data were consistent with a twofold range in F (Alverson et al. 1987)).

One can conclude that constraints imposed by the DFO stifled efforts to undertake, or to discuss publicly, such analyses of scientific uncertainty. These constraints took various forms. Prominent among them was the withholding of research survey data from DFO scientists who did not normally participate in the annual stock assessments (see Finlayson 1994). Scientists were also explicitly ordered then, as they are today, not to discuss "politically sensitive" matters (e.g., the status of fish stocks currently under moratoria) with the public, irrespective of the scientific basis, and publication status, of the scientist's concerns. These constraints are on record in the form of memoranda between DFO officials and DFO scientists (e.g., memorandum dated 6 June 1995).[1]

Bias in stock status reports and manipulation of public perception

Bias is evident in some Stock Status Reports published by the DFO. These documents, written for public distribution, summarize contemporary scientific knowledge of the fish stocks managed by the DFO. They are also meant to reflect the Department's "scientific consensus" regarding the status of the various stocks.

The 1995 Groundfish Stock Status Report for Newfoundland Region begins with a seven-page Overview of the groundfish fisheries. Much of this Overview focuses on the causes of the recent stock collapses (the remainder provides brief descriptions of the fisheries for groundfish, pelagic fish, and invertebrates, harp seal abundance estimates, and trends in water and air temperatures). In this regard, one would reasonably expect a balanced treatment of the scientific research that has investigated the reasons for the stock collapses and to identify all relevant scientific documents upon which this research is based.

The 1995 Stock Status Report for Newfoundland groundfish does neither. The potential influence of fishing on the groundfish collapse receives almost no mention in the Stock Status Report's Overview, being limited to the remark that "while some strongly advocate that the decline can be fully explained by fishing, others believe there was an important environmental component that must not be ignored" (DFO 1995*a*, p. 5). Roughly half of the Overview is then devoted to arguments in support of some form of environmental or ecosystem change as an important cause of the stock declines. Virtually none of the evidence that fishing was the primary cause of the stock declines is presented in the document. This explicit bias is even more apparent when one is aware that work documenting overfishing of northern cod was excluded from the 1995 Stock Status Report despite the fact that such research had either been published (e.g., Hutchings and Myers 1994), presented at pre-1995 assessment meetings (e.g., Myers and Cadigan 1995*a*, 1995*b*), or presented at the April 1995 stock assessment meeting in St. John's (e.g., Myers et al. 1996*a*, 1996*b*, 1997*a*; see Shelton 1996).

Thus, the DFO's 1995 Stock Status Report for Groundfish in the Newfoundland Region inaccurately reflected the breadth of research that had been conducted on the causes of the groundfish collapses. Clearly, then, it did not represent a consensus among scientists who were conducting research in the area, although it may have represented a consensus of sorts among those who contributed to the final document.

A second example of selective exclusion of scientific information is the 1995 Stock Status Report on Gulf of St. Lawrence groundfish (DFO 1995*b*). The commercial fisheries for Gulf cod were closed in September 1993. The scientific document upon which the status of southern Gulf cod was based (Sinclair et al. 1995) was written after assessment meetings held in March 1995. This document noted that the 1993 closure of this fishery was attributable to the low abundance of 6- to 8-year-old cod — the age classes that usually comprise the bulk of the commercial catch. Sinclair et al. (1995) examined the degree to which the high mortality experienced by the 1985, 1986, and 1987 year classes of cod was due to fishing, seal predation, and environmental conditions. They concluded that "the most likely cause is increased exploitation in the late 1980's and early 1990's" (Sinclair et al. 1995, p. 25) and provided evidence in support of this conclusion. With respect to seals, "based upon current information [on survey-based trends in cod mortality], it is unlikely that Grey seal predation was the main cause of this trend in mortality" (Sinclair et al. 1995, p. 25). Regarding environmental causes of increased cod mortality, based on temporal trends in "the most severe environmental indicator in the southern Gulf of St. Lawrence," Sinclair et al. (1995, p. 25) concluded that "it is also unlikely that unfavorable environmental conditions are primarily responsible for this pattern [i.e., increased mortality of 1985–87 year classes]."

---

[1] Complete set of data (memoranda) available for a minimal charge from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Bldg. M-55, Montreal Road, Ottawa, ON K1A 0R6, Canada.

Thus, the conclusion reached during the 1995 assessment of southern Gulf cod was that the high mortality experienced by the year classes of cod that should have supported the fishery in the early 1990s was due to high fishing mortality. Observed trends in grey seal abundance and physical oceanographic conditions were apparently inconsistent with hypotheses that attributed increased cod mortality to either of these factors. The following statement was part of the original draft of the Stock Status Report submitted for approval to DFO officials in Ottawa and was to have appeared on p. 15 as part of the Regional Overview of fish stocks (memorandum dated 15 June 1995):

> "It is unlikely that seal predation or environmental conditions are responsible for these trends in total mortality [of the 1985–87 year classes of cod]."

The Assistant Deputy Minister (DFO Science) asked, "Is there evidence to back up this statement and is it consistent with last year's statement on grey seals?" (memorandum dated 15 June 1995). The Regional response to this query from Ottawa was to remove the statement from the Stock Status Report, contrary to scientific advice that the statement had empirical support and that it should remain (memorandum dated 15 June 1995).

Fishing people and the Canadian public have been ill-served by the bias that can exist in Stock Status Reports. The public has every right to expect such reports to represent the current state of knowledge of the groundfish stocks and the factors that influence fish abundance. Because of the authoritative profile that the Stock Status Reports assume, the public might well believe that these documents represent a consensus among fisheries scientists. Instead, as is clear in the aforementioned 1995 Stock Status Reports on Atlantic groundfish, recent key reviews have been biased against research that has identified overfishing as the primary cause of the present stock collapses.

Use of the "scientific consensus" of stock status reports to influence fisheries scientists

An indirect but equally serious effect of bias in Stock Status Reports has been on the research conducted by fisheries scientists. One example serves to illustrate this point. In response to questions asked by a journalist, a DFO research scientist in Newfoundland was quoted as saying "what happened to the [East Coast] fish stocks had nothing to do with the environment, nothing to do with seals. It is simply overfishing" (Globe & Mail, 25 August 1995). These comments were consistent with much of the research that had been conducted and published in peer-reviewed scientific journals. This includes articles on the collapse of northern cod (e.g., Hutchings and Myers 1994, 1995; Myers and Cadigan 1995*a*, 1995*b*; Hutchings 1996; Myers et al. 1996*a*, 1996*b*, 1997*a*; Walters and Maguire 1996; Walters and Pearse 1996; Sinclair and Murawski 1997; R.W. Doyle et al., unpublished data) and on other North Atlantic cod stocks (Myers et al. 1996*b*; Cook et al. 1997; Sinclair and Murawski 1997). It also agrees with the conclusions reached at the March 1995 assessment meetings on southern Gulf cod (Sinclair et al. 1995). However, as a consequence of this quote, the DFO scientist in question received an official reprimand for making statements that were not consistent with the content of the 1995 Stock Status Report for Newfoundland Groundfish (DFO 1995*a*) (memorandum dated 7 September 1995):

> "Your comments, as presented by the media, did not give a balanced perspective on the issue of the status of the cod stocks and were inconsistent with the June 1995 Newfoundland Stock Status Report. [We] have cautioned you regarding statements which do not take into account peer-reviewed scientific information. Your...disregard for both departmental policy on communication with the media and the professional opinions of your colleagues warrant the disciplinary action of a written reprimand. In the future, you are expected to respect both the system of primary spokespersons and peer conclusions on matters within your area of expertise."

By making public statements consistent with scientific publications (anonymously peer-reviewed) to which he also contributed, a fisheries scientist was officially reprimanded and experienced the job insecurity and psychological stress that accompany such reprimands. Bureaucratic action of this kind cannot help but have a stifling effect on proper conduct of science in the organization. Freedom to raise scientific debate should be integral to the conservation and management of Canada's natural resources.

Legitimization of bureaucracy: the portrayal of "science" as science

Inclusion of fisheries science within a political body can permit analyses presented by that body to be portrayed as being based on science, thereby legitimizing government policy and Departmental objectives. One example of such legitimization occurred in July 1992 when the DFO announced that a moratorium would be imposed on commercial fishing for northern cod. The moratorium was expected to last 2 years (DFO 1992). This 2-year time frame provided the temporal basis for the income support package (Northern Cod Adjustment and Recovery Program) that the Canadian Government offered fishing people affected by the fishery closure. What was the scientific basis of this 2-year recovery period?

The 2-year time frame for the recovery of northern cod was apparently based on a graph in a government press release (DFO 1992; reproduced as Fig. 10 in Lear and Parsons 1993). The graph in the press release provided two projected increases in northern cod spawner biomass between 1992 and 1994. The projections indicated that, in the absence of fishing, northern cod spawner biomass would increase *more than sixfold* between 1992 and 1994 to as much as 600 000 t — a spawner biomass that had not existed since 1972. These projections appear to have been made by (1) multiplying the 1992 numbers-at-age vectors estimated from two Virtual Population Analyses (VPAs) (ADAPT and Laurec–Shepherd) by a mean weight-at-age vector and (2) assuming that the instantaneous rate of total mortality on northern cod during that period would be caused by natural factors alone (i.e., $Z = M = 0.2$).

These spawner biomass projections portray data as having a scientific basis despite being subjected to none of the criteria that are part of a complete scientific analysis (e.g., anonymous peer review). For example, the scientific literature contains estimates of instantaneous rates of population increase (r) considerably lower than those required by the DFO (1992; Table 1). The values of r associated with the DFO's projected population increases range from 0.80 to 1.10, corresponding to annual rates of increase in spawner biomass at low density of 126 and 200%, respectively. In contrast, estimates of r in the scientific literature for northern cod range from 0.09 to 0.17, corresponding to annual rates of increase of 9 and 19%, respectively. Moreover, only 3 (15%) of the 20 cod stocks throughout the North Atlantic are predicted to have values of r in excess of 0.80. In each of these 3 stocks, age at maturity is 2 to 3 years rather than the 6–7 years for northern cod (Myers et al. 1997*b*). Thus, the DFO estimates differ markedly from studies published in the scientific literature based on data available in 1992.

The DFO labelled its two projections of spawner biomass as "high" and "low." This suggests a statistically based confidence interval, i.e., a reflection of the error associated with a mean projection. Instead, the "high" predicted spawner biomass referred to the ADAPT-based projection, while the "low" estimate was that based on the Laurec–Shepherd method. This can only be determined from the original stock assessment document in which the VPA estimates were calculated (Baird et al. 1992, Table 46). Thus, statistical confidence intervals, a normal calculation in the scientific literature, were not part of the DFO's predicted 2-year moratorium period. Finally, the DFO's spawner biomass predictions were based on the assumption that the most recent VPA estimates of age-specific abundance were without error. This assumption has been demonstrated repeatedly to be without justification and to produce grossly inaccurate estimates of future stock biomass (Walters and Maguire 1996; Walters and Pearse 1996).

Summary

The perceived need for scientific consensus and an "official" position has seriously limited the effectiveness of government-based research to contribute effectively towards an understanding of the collapse of Atlantic cod. Nonscience influences on fisheries research incompatible with normal scientific inquiry included (*i*) government denunciation of independent work, (*ii*) misrepresentation of alternative hypotheses, (*iii*) interference in scientific conclusions, (*iv*) disciplining of scientists who communicated publicly the results of peer-reviewed research, and (*v*) misrepresentation of the scientific basis of public reports and government statements.

Pacific salmon production in British Columbia: the Kemano Completion Project

Prologue

Inappropriate government influence on fisheries science in Canada is also evident on the Pacific coast. A well-documented example is the September 1987 Nechako Settlement Agreement between the DFO, the Province of British Columbia, and ALCAN. The central focus was the rate of water discharge from an ALCAN dam. The water temperature and flow conditions provided by the discharge were biologically important to salmonid production in the Nechako River, B.C. The Nechako River, a major tributary of the Fraser River, had a mean annual discharge (MAD) of 201.9 $m^3 \cdot s^{-1}$ (Jaremovic and Rowland 1988) and supported several salmonid fish including sockeye, *Oncorhynchus nerka*, and chinook salmon, *Oncorhynchus tshawytscha*.

In the early 1950s, the B.C. Government gave permission to ALCAN to construct an aluminum smelter in Kitimat, B.C. They built a water storage and hydro-generating dam to supply electric power. The dam greatly reduced water flows in the Nechako River. Between the late 1950s and 1978, operation of the dam reduced annual discharges by 40–50%. Low reservoir inflows coupled with increased demand for electricity in 1979 resulted in the release by ALCAN of even lower water flows (November 1979 discharge was approximately 10% of natural flows; BCUC 1994).

In 1980, the Attorney General of Canada obtained, on behalf of the DFO, a temporary injunction from the B.C. Supreme Court that required ALCAN to release flows that averaged about 33% of natural flows (60.9 $m^3 \cdot s^{-1}$; DFO 1986). In mid 1985, ALCAN petitioned the B.C. Supreme Court for a permanent resolution to the jurisdictional issues regarding discharge rates in the Nechako River. A trial was set for the end of March 1987.

In preparation for the trial, the DFO wanted a definitive position on the discharge necessary to protect salmonid populations in the Nechako system. A briefing document provided to the Minister of Fisheries and Oceans in preparation for a 24 February 1986 meeting in Vancouver suggested two alternative flow regimes: a "base" flow regime of 62.8 $m^3 \cdot s^{-1}$ (DFO 1986) and a "preferred" flow regime of 124.0 $m^3 \cdot s^{-1}$ that made use of surplus water in wet years (BCUC 1994). It was the view of several DFO scientists who had, since 1983, been assessing the influence of river discharge on salmonid survival and production in the Nechako River that flows in the range of the preferred flow and higher were required to maintain salmonid production at conservation targets (BCUC 1994). Following the 24 February 1986 meeting, the Minister indicated that he "was not satisfied with the pleading [i.e., the preferred flows]." This was partially because of the uncertain fishery benefits provided by the additional flows and the natural hydrological variability in ALCAN's water supply. The Minister requested that the pleading be made "more reasonable" (memorandum dated 25 February 1986). Following a recommendation made by the Deputy Minister (memorandum dated 27 February 1986), the DFO revised its pleading to indicate that it sought a requirement for ALCAN to adopt the base flow, the lower of the flow regimes considered by the DFO. By comparison, ALCAN's pleading flows before the Supreme Court (MAD of 19.6 $m^3 \cdot s^{-1}$; DFO 1986) represented approximately one third the 1980 "injunction" rate recommended by DFO.

In March 1987, the B.C. Government pressed for an out-of-court settlement (BCUC 1994). The Minister of Fisheries and Oceans agreed. Following a series of proposals and counter-proposals between the DFO and ALCAN, negotiations culminated in a 4-day meeting between representatives of the DFO, ALCAN, and the B.C. Government. The Terms of Reference for this Nechako River Working Group (NRWG) were, "To develop a program of measures and plan of implementation which will provide an acceptable level of certainty for the conservation and protection of the chinook fisheries resource

Table 1. Predicted rates of population increase (r) for northern cod, based on data available in 1992; this table contrasts official predictions by the DFO (1992) with those published or submitted to the scientific literature.

Type of analysis	Population growth (r)	Reference
ADAPT VPA	0.80–0.88	DFO 1992
Laurec–Shepherd VPA	0.98–1.10	DFO 1992
Age-specific survival and fecundity	0.13–0.17	Hutchings and Myers 1994
Stock–recruitment relationship	0.17	Myers et al. 1997*b*
Stock–recruitment relationship and population growth analysis	0.09–0.13	Walters and Maguire 1996

of the Nechako River" (BCUC 1994). However, the discharge rates being considered by the NRWG differed considerably from those previously pleaded by the DFO to the Supreme Court. In fact, the NRWG was instructed to "take the Alcan fish and other use flows as a given" (BCUC 1994, p. 28). One interpretation of this instruction is that the DFO was asking if there was an acceptable way of adopting ALCAN's low discharge rates (approximately 10% of historical flows and about one third of the DFO's pleading rate). The NRWG identified a hierarchical series of mitigative measures (ranging from habitat improvements to the construction of a hatchery) intended to ensure an escapement of 3100 chinook spawners per year (i.e., the 1980–1986 average escapement, identified by the NRWG as a conservation target) (BCUC 1994). The result of the deliberations by the NRWG was the Nechako Settlement Agreement, announced by the DFO in September 1987, in which a long-term flow regime (26.5 $m^3 \cdot s^{-1}$), slightly greater than ALCAN's pleading flows, was accepted and a series of measures intended to mitigate unintended effects of low flows on salmonid production presented.

Bureaucratic interference in the interpretation and dissemination of scientific research

Following the imposition of the injunction flow in 1980, ALCAN undertook an environmental impact assessment of the Kemano Completion Project (KCP). This expansion project would permit ALCAN to utilize all of the water it was entitled to under its original contract with the B.C. Government. In August 1983, a team of DFO biologists and scientists — the Kemano Task Force — was formed "to co-ordinate and conduct the technical review of ALCAN's proposal from a biological perspective, assist in developing the departmental position on the proposed development and provide technical assistance at public hearings" (Mundie 1994, p. 4; Schouwenburg 1994). The Task Force concluded in March 1985 that ALCAN's proposed flow (ALCAN's eventual pleading flow) would adversely affect chinook salmon in the Nechako River (Schouwenburg 1994). The Task Force Report also made it clear that "there were few areas of agreement between the positions taken by ALCAN's consultants and the Task Force regarding the extent and nature of the impacts on the fisheries resource arising from the project" (Schouwenburg 1994, p. 4).

In preparation for the DFO's Supreme Court case against ALCAN, a workshop was held in mid-November 1985 at which the potential biological consequences of ALCAN's proposed flow regime were discussed (BCUC 1994). The proceedings of this workshop marked "the first time that scientists began to entertain a suspicion that the Department might not be solely concerned with providing flows that would protect the salmon" (Mundie 1994, p. 7). One of the scientists' concerns was the proceedings' failure to document adequately the differences in opinion that existed between scientists and managers. As noted by one scientist (memorandum dated 28 November 1985, italics added):

> "I am greatly disturbed generally by the failure of the [workshop's] notes to accurately record the polarization of opinions which occurred between the scientists and the habitat managers...the scientists were using as a starting point the amount of water required for the needs of the fish while the managers were starting from the point of optimizing conditions for the fish with water left over after water was first used for hydroelectric generation."

In mid-February 1986, just prior to the Minister's aforementioned 24 February meeting in Vancouver, three of the scientists who had been members of the Kemano Task Force expressed their discontent with the Technical Report being prepared to brief the Minister, noting the "substantial differences that exist between the views expressed in the report...and those offered by us" (memorandum dated 13 February 1986). In their opinion, "the gap between scientists and the operational staff in this matter is one that [can] not be bridged by minor adjustments in the report, but only by a major re-aligning of approach, i.e. away from compromise with industry and towards defining safe conditions for the fish" (memorandum dated 13 February 1986). It could be argued that the opinions of the scientists simply reflected one end of a continuum of opinions that ranged from having a wholly "natural system" to making every attempt to accommodate industry, recalling that habitat managers do have to deal with industry on a regular basis. It could also be argued that it was at this point in time that the selective use of available scientific information began, perhaps reflecting an editorial role that management staff had on the preparation of the Minister's briefing document.

The influence of the Kemano Task Force was further eroded at the 24 February 1986 briefing of the Minister at which no DFO research scientist was present (memorandum dated 25 February 1986). Recall that the two potential pleading discharge rates being considered by the DFO were the base flow of 62.8 $m^3 \cdot s^{-1}$ and the preferred flow regime of 124.0 $m^3 \cdot s^{-1}$ (BCUC 1994). Following the meeting, a senior ministerial bureaucrat concluded, "we [i.e., those who prepared the report for the Minister] were being unreasonable in our demands to take all the excess water [in wet years] to obtain questionable benefits in fisheries production" (memorandum dated 25 February 1986). The pleading was revised and the Minister adopted the base flow regime as the DFO's pleading flow in the file submitted to the B.C. Supreme Court on 28 February 1986 (BCUC 1994).

The selective inclusion of, or emphasis placed on, the scientific input that supported the Minister's decision to set the pleading flows at the base flow rate was noted by those who had participated in the Kemano Task Force (Mundie 1994). The 1986 briefing report failed to document scientific uncertainty that the base flows would achieve the conservation goal of salmon production. Rather, the document indicated certainty that the base flow was the minimum acceptable flow, and that somewhat uncertain benefits might result from higher (i.e., the preferred) flows. In response to a query by one of the Task Force scientists as to the origin of the final pleading flows, the senior DFO manager responsible for the Nechako River Project wrote, "If you are referring to the current pleading flows I am sure you are aware that those flows represent the Minister's opinion not any decision of our team" (memorandum dated 4 March 1987).

Between March 1986 and March 1987, the DFO prepared expert reports and expert witness statements for the trial (BCUC 1994). But despite being asked to provide scientific input to the court case in the form of witness statements, science was not to be the first priority of DFO research scientists. Rather, their first priority was that they support the Minister's position. This is perhaps not surprising given the need of lawyers to marshall all available evidence to support the Minister's decision. However, this highlights the dilemma between the scientific ethos of basing opinion on empirical "facts" and the need of a government department to support its Minister. Regarding his role as a potential expert witness, one of the scientists of the Kemano Task Force asked, "How can a scientist who opposed the recommended flows both before and during the time they were being drawn up speak for them?" (memorandum dated 18 July 1986). Referring to bureaucratic interference on the contents of expert witness statements, this scientist noted (memorandum dated 18 July 1986):

> "At a meeting in Vancouver on April 28 the Director General instructed staff to support the Minister's position while adhering to the scientific advice. As my statement shows, I find it impossible to do both...[It was] pointed out to me that those technical staff who do not support the Minister 'must take their game and play elsewhere'. This underlines the seriousness of my predicament and makes me feel intimidated."

Following the request by the B.C. Government for an out-of-court settlement, there was no more need for expert witness statements. That much of the scientific evidence and expertise available to the Department was ignored is evidenced by the NRWG terms of reference in 1987, and by the decision to exclude most of the individuals intimately involved with the project from the Working Group.

Evaluations by scientists

Since the announcement of the Agreement, the mitigative measures described therein have been denounced by the independent Commission, chaired by Dr. Peter Larkin, that undertook the Kemano Completion Project Review in 1994 (BCUC 1994, pp. 156–157):

> "The various proposed instream remedial measures are for the most part untried and in the view of the Commission will not be effective as mitigation. The proposed measures for protection of resident trout...are at least as unlikely to be effective as those for chinook salmon as measures of mitigation. The concept of off-site mitigation...is unacceptable because it does nothing to replace the habitat that is lost."

The arguments by DFO scientists for high water discharge rates appear to have been well founded. They were supported at the time by a case history study by Mundie and Bell-Irving (1986) that documented reductions in the salmon stocks in 26 of 29 rivers in which flows had been regulated. And more recently, Bradford (1994) has suggested that there is evidence of a negative association between flow and chinook salmon production in the Nechako River. His work also questions the capability of the current flow regime to sustain the chinook population at the 3100 spawner target identified in the Settlement Agreement.

Summary

The selective use of scientific information in the events leading to, and in the provisions contained within, the Nechako Settlement Agreement of September 1987 is a poignant example of how government bureaucrats can, and do, interfere with science. Decisions on flow regimes were made and were termed scientifically defensible despite a broad range of scientific opinion to the contrary. These problems are well summarized by one of the biologists originally involved in the assessment of the KCP in a brief prepared for the 1994 Kemano Completion Project Review (Schouwenburg 1994, p. 12):

> "The facts of the matter are that [the Minister] and his government chose...to adopt a position of virtual surrender to both ALCAN and the province. They did not...admit that this was what had been done and chose instead to embark on a program of disinformation. First they had to disavow the existence of credible information contrary to ALCAN's view of the impacts of the project. This was accomplished through [1] the suppression of information such as that contained in the Kemano Task Force Report, [2] the intimidation and 'gagging' of employees familiar with the project evaluations done by DFO with respect to the Task Force and the court case to the point that they fear for their jobs, and, [3] the misrepresentations of the terms of reference given DFO representatives to the [NRWG] in recommending the Nechako Settlement Agreement."

Restructuring the linkage between science and management of fisheries

One factor common to the examples given above, intentional or otherwise, and to greater or lesser degrees, is a suppression of scientific uncertainty. We would argue that bureaucratic intervention has deleteriously influenced the ability of scientists to contribute effectively to fisheries management. Viability of fish stocks, sustainability of employment in fisheries, and persistence of coastal fishing communities would appear to be poorly served by the present institution in which fisheries science is inextricably linked to, and affected by, a political bureaucracy. It is difficult to imagine how wise policies for dealing with uncertainty can be devised in the present administrative atmosphere.

We suggest that the science and stock assessments conducted for government be provided by a publicly funded, but politically independent, institution (somewhat analogous to the Canadian judiciary). The former Canadian fisheries research boards (e.g., Biological Board of Canada (1912–1937), FRB (1937–1979)) may provide an appropriate model of an organization of fisheries scientists dedicated to undertaking research on the population biology of commercially exploited fishes.

The precursor to the Biological Board was the Board of Management of the Marine Biological Station of Canada. Established in 1898, the Board consisted of one representative of the Canadian Department of Fisheries and eight professors from each of eight universities whose faculty collaborated with Board researchers in fisheries research (Johnstone 1977). The objectives of this Board, and of its successors, were twofold: (*i*) to undertake independent scientific research on aquatic organisms in marine and inland waters and (*ii*) to provide solutions to practical and applied problems in the commercial fisheries.

In 1912, protests by the Board and its researchers against government control of the Board's research budget resulted in the formation of the more independent Biological Board of Canada (Johnstone 1977). Oversimplifying the situation, but identifying one of the scientists' seeds of discontent, A.G. Huntsman recalled that (Huntsman 1943, italics added)

> "A clerk's veto of a request for purchase of scientific literature because the latter was in foreign languages caused an explosion and resulted in the creation in 1912 by Act of Parliament of the Biological Board of Canada, an *independent* body under the Minister to have charge of all [Canada's] biological stations."

The scientific value of the Biological Board and its researchers was rated highly by scientific peers. For example, University of Toronto zoologist J.R. Dymond noted in 1939 that, "no other factor has had a greater influence on the development of zoology in Canada than the organization of the Biological Board" (Dymond 1939, p. 49). The Biological Board consisted of 12 members: two representatives of the Canadian Department of Fisheries, two representing the fishing industry, and eight nominated by as many Canadian universities. Dymond noted that whereas the Biological Board stressed representation of universities, the 1937 Act that created the FRB permitted the selection of scientists "peculiarly suitable for the Board's work, the institution to which they may happen to be attached being a secondary matter" (Dymond 1939, p. 51). The FRB in the late 1930s consisted of nine scientists, four representatives of the fishing industry, and two Department of Fisheries representatives; its permanent scientific staff consisted of approximately 35 individuals (Dymond 1939).

The formation of the International Commission for the Northwest Atlantic Fisheries (ICNAF) in 1949 stimulated an increase in the effort expended by the FRB on matters related to stock assessments; fish behaviour and fishing methodology were apparently studied seriously for the first time (Johnstone 1977). The scientific excellence of the FRB in the 1950s and 1960s is evident from a sampling of its members: F.E.J. Fry, J.L. Hart, F.R. Hayes, W.S. Hoar, D.R. Idler, P. Larkin, W.E. Ricker, and W. Templeman. However, with a restructuring of the Department of the Environment in the early 1970s, increasing government infringement on the operations of the FRB culminated in 1972 when the Board lost its independent status, reporting thereafter to an Assistant Deputy Minister for Marine and Fisheries (previously the FRB had reported directly to a Minister). F.R. Hayes, Chair of the FRB from 1964 to 1969, argued that the primary reason for government's desire for increased influence of fisheries research was that "the government simply cannot contemplate the control of policy and funds by any but its own employees" (Hayes 1973, p. 31). The FRB was dissolved by an Act of Parliament in 1979 with the consolidation of fisheries research in the newly created Department of Fisheries and Oceans.

Proposed solutions

Recognizing the need for recuperative measures, what would be the attributes of a new natural resource science establishment that could operate unimpeded by bureaucratic and political influence? This new organization would provide scientific information on issues such as abundance and stock status of exploited fish stocks, effect of habitat alteration on fish production, and deleterious consequences of interactions between wild and cultured fishes to the Minister of Fisheries and Oceans but would not be a part of that Department. The organization would meet annually to prepare assessment documents and stock status reports in much the same way that DFO biologists and scientists do today. But critical differences would include the following, using stock assessments as an example.

(*i*) Assessment documents would be explicit concerning scientific disagreements about stock status. This could take the form of the presentation of different sets of assumptions concerning the stock and the abundance and fishing mortality corresponding to each set. The review process would produce decision tables showing the range of ecological consequences (alternative hypotheses about response) for a strategic range of alternative strategies (Hilborn et al. 1993). The presentation would examine possible outcomes for a range of strategies, ordered from very cautious to very optimistic. The review process would also include highly qualified ecologists and population biologists regardless of the "fisheries application" of their research.

(*ii*) The variability associated with model parameters and variables used in each analysis would be quantified and made explicit in the document.

(*iii*) All scientific information on stock abundances would be released to the public at the same time that it was presented to the DFO. This point is extremely important; by making all scientific information available to the public, the public could then evaluate for themselves the Minister's management decisions based on the scientific data that had been received. The public cannot at present make such an evaluation, making it possible for politicians and fishery managers to disregard scientific advice on occasion and to blame unintended consequences of such management decisions on the quality of the scientific information given to them on other occasions (Finlayson (1994) discusses and gives examples of such instances in more detail). Such a model of interactions between scientists and managers/politicians would do considerably more in providing an objective scientific basis to fishery management than does the present structure of the DFO (see also Walters 1995). It is not clear how such a reorganization would

Table 2. Arbitrary probabilities of occurrence of six undesirable influences on the conduct and communication of fisheries science and stock assessments under different institutional arrangements.

	Assessments/science/ fisheries policy conducted by government department (status quo)	Strengthened external review of assessments and policy options	Contested assessments by interested groups	Alternative assessments by different national or international organizations (e.g., ICES, NAFO)	Privately funded, contracted assessments/science	Publicly funded, politically independent science/policy analysis organization
Failure to transmit scientific uncertainty to decision makers	Medium/high	Low/medium	Low	Low	Low/medium	Low
Inability or unwillingness of decision makers to acknowledge or address scientific uncertainty	Medium/high	Medium	Medium	Low/medium	Medium/high	Low/medium
Government restriction of public access to assessment/science data	Medium/high	Medium/high	Low/medium	Medium/high	Medium/high	Low
Government interference in public dissemination of scientific research	Medium/high	Medium/high	Medium/high	Medium/high	Medium/high	Low
Government influence on direction of scientific research	Medium/high	NA	NA	NA	Medium/high	Low
Industry interference in public dissemination of scientific research	Low	Low	Low/medium	Low	Medium	Low

be initiated, but it would be unlikely to occur without a comprehensive public examination (e.g., Report by the Auditor General for Canada) of the present structure of the DFO and of the factors that compromise its mandate for the conservation of fish.

Being the most preferable change in the status quo, the formation of a publicly funded body of scientific inquiry, completely independent of political influence, is one of a range of modifications to the present system that could be implemented. A representative, but by no means exhaustive, set of options is offered in Table 2. These include (*i*) contested stock or habitat assessments for which different parties, such as commercial and recreational fishers, industry representatives (e.g., ALCAN), and conservation groups, participate in the assessment process, have full access to the raw data, and analyze and table alternative assessments for decision makers if a consensus is not reached, (*ii*) alternative assessments conducted by different national laboratories or international organizations, and (*iii*) privatized research in which independent research organizations are contracted to undertake specific assessment tasks or narrowly defined research projects. To each of these options, we have assigned arbitrary, but perhaps not unreasonable, probabilities of occurrence of six institutional factors considered undesirable in fisheries science and fisheries management. Such a table may provide a useful starting point for discussion (see also Hilborn et al. 1993). Detailing the means by which each of these institutional structures would deal with the problems identified would be an appropriate subject of a separate paper.

Summary

We have given two examples of how nonscience influences can interfere with scientific information and the undertaking and conduct of fisheries research in the Canadian Department of Fisheries and Oceans. The present framework for linking science with management can, and has, lead to abuses that threaten the ability of scientists to understand fully the causes of fish declines, to identify means of preventing fishery collapses from recurring, to incorporate scientific advice in management decisions, and to communicate research in a timely fashion to as wide an audience as possible. The existing framework of government-sponsored fisheries science needs to be replaced. It has failed to ensure viable fish resources and thereby sustain the fishing people and fishing communities upon which successful fisheries management depends. The economic and societal cost of this failure to Canada has been enormous.

The present work invites a variety of questions about why the federal government, or at least the part represented by the DFO, has acted in the manners described above. Why were senior DFO officials not interested in ensuring wide reporting of differences of opinion about assessment matters? Why did they repress challenges to their practices, given that the biological and socioeconomic consequences would be extremely serious if DFO assessments were indeed optimistic? To what degree were decisions based on individual differences in personality, or perhaps the perceived need to balance scientific concerns with the sociopolitical constraints imposed on the decision-making process by a government bureaucracy?

There is a clear and immediate need for Canadians to examine very seriously the role of bureaucrats and politicians in the management of Canada's natural resources. The present framework of government departments such as the DFO is based on the belief that the conservation of natural resources is best ensured by science integrated within a political body. Recent history would suggest otherwise The formation of a politically independent organization of fisheries scientists, or some such reorganization of the link between scientific research and the management of natural resources, is a timely idea that merits immediate, serious, and open debate.

Acknowledgments

The fisheries research programmes of the authors are supported by NSERC (Canada) Research Grants and by a Tri-Council Eco-Research Project (NSERC, SSHRC, MRC) grant (J.A.H. and R.L.H.). We thank Nicholas Flanders, Brian Hall, Ray Hilborn, Steve Kerr, Marty Leonard, Ian McLaren, Douglas Morris, Gary Sharp, Peter Sinclair, and seven DFO employees involved in stock assessment and fisheries research for their critical comments and discussion. Memoranda cited herein were available either through Canada's Access to Information Act or as exhibits prepared for the 1994 commission on the Kemano Completion Project Review conducted by the British Columbia Utilities Commission.

References

AGAC (Atlantic Groundfish Advisory Committee). 1990. Summary minutes of the Atlantic Groundfish Advisory Committee meeting, 25–26 October 1990, Ramada Renaissance, Montreal, Que.

Alverson, D.L., Beamish, F.W.H., Gulland, J., Larkin, P., and Pope, J. 1987. A study of trends of cod stocks off Newfoundland and factors influencing their abundance and availability to the inshore fishery. Task Group on Newfoundland Inshore Fisheries. Report to the Minister of Fisheries and Oceans, Ottawa, Ont.

Baird, J.W., and Bishop, C.A. 1986. Assessment of the cod stock in NAFO Divisions 2J+3KL. NAFO SCR Doc. 86/47.

Baird, J.W., and Bishop, C.A. 1987. Assessment of the cod stock in NAFO Divisions 2J+3KL. NAFO SCR Doc. 87/42.

Baird, J.W., Bishop, C.A., and Murphy, E.F. 1991. Sudden changes in the perception of stock size and reference catch levels in Northeastern Newfoundland Shelves. NAFO Sci. Counc. Stud. **16**: 111–119.

Baird, J.W., Bishop, C.A., Brodie, W.B., and Murphy, E.F. 1992. An assessment of the cod stock in NAFO Divisions 2J3KL. NAFO SCR Doc. 92/18.

BCUC. 1994. Kemano completion project review. Report and recommendations to the Lieutenant Governor in Council, British Columbia Utilities Commission, Vancouver, B.C.

Bradford, M.J. 1994. Trends in the abndance of chinook salmon (*Oncorhynchus tshawytscha*) of the Nechako River, British Columbia. Can. J. Fish. Aquat. Sci. **51**: 965–973.

CAFSAC. 1986. Advice on the status and management of the cod stock in NAFO Divisions 2J, 3K and 3L. CAFSAC Adv. Doc. 86/25.

CAFSAC. 1990. Advice on the management of groundfish stocks. CAFSAC Adv. Doc. 90/5.

Cashin, R. 1993. Charting a new course: towards the fishery of the future. Communications Directorate, Department of Fisheries and Oceans, Ottawa, Ont.

Cell, G.T. (*Editor*). 1982. Newfoundland discovered: English attempts at colonisation, 1610–1630. The Hakluyt Society, London.

Cook, R.M., Sinclair, A., and Stefánsson, G. 1997. Potential collapse of North Sea cod stocks. Nature (Lond.), **385**: 521–522.

DFO. 1986. Nechako River, British Columbia. Flow requirements for fish and fish habitat. Regional Technical Position of the Department of Fisheries and Oceans, 10 February 1986. Exhibit 355, Kemano Completion Project Review, British Columbia Utilities Commission, Vancouver, B.C.

DFO. 1992. Crosbie announces first steps in northern cod (2J3KL) recovery plan. News Release, 2 July 1992. NR-HQ-92-58E.

DFO. 1995*a*. Report on the status of Canadian managed groundfish stocks of the Newfoundland region. DFO Atl. Fish. Stock Status Rep. 95/4E.

DFO. 1995*b*. Compilation of the reports on the status of groundfish stocks of the Gulf of St. Lawrence. DFO Atl. Fish. Stock Status Rep. 95/5E.

Dymond, J.R. 1939. Zoology in Canada. *In* A history of science in Canada. *Edited by* H.M. Tory. Ryerson Press, Toronto, Ont. pp. 41–57.

Finlayson, A.C. 1994. Fishing for truth: a sociological analysis of northern cod stock assessment from 1977–1990. Inst. Social Econ. Res., Memorial University of Newfoundland, St. John's, Nfld.

Hayes, F.R. 1973. The chaining of Prometheus: evolution of a power structure for Canadian science. University of Toronto Press, Toronto, Ont.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment. Chapman and Hall, New York.

Hilborn, R., Pikitch, E.K., and Francis, R.C. 1993. Current trends in including risk and uncertainty in stock assessment and harvest decisions. Can. J. Fish. Aquat. Sci. **50**: 874–880.

Huntsman, A.G. 1943. Fisheries research in Canada. Science (Washington, D.C.), **98**: 117–122.

Hutchings, J.A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Can. J. Fish. Aquat. Sci. **53**: 943–962.

Hutchings, J.A., and Myers, R.A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Can. J. Fish. Aquat. Sci. **51**: 2126–2146.

Hutchings, J.A., and Myers, R.A. 1995. The biological collapse of Atlantic cod off Newfoundland and Labrador: an exploration of historical changes in exploitation, harvesting technology, and management. *In* The North Atlantic fishery: strengths, weaknesses and challenges. *Edited by* R. Arnason and L.F. Felt. Inst. Island Stud., University of Prince Edward Island, Charlottetown, P.E.I. pp. 37–93.

Jaremovic, L., and Rowland, D. 1988. Review of chinook salmon escapement in the Nechako River, British Columbia. Can. MS. Rep. Fish. Aquat. Sci. No. 1963.

Johnstone, K. 1977. The aquatic explorers: a history of the Fisheries Research Board of Canada. University of Toronto Press, Toronto, Ont.

Keats, D., Steele, D.H., and Green, J.M. 1986. A review of the recent status of the northern cod stock (NAFO Divisions 2J, 3K, and 3L) and the declining inshore fishery. A report, to the Newfoundland Inshore Fisheries Association, on Scientific Problems in the Northern cod controversy, St. John's, Nfld.

Lear, W.H., and Parsons, L.S. 1993. History and management of the fishery for northern cod in NAFO Divisions 2J, 3K and 3L. *In* Perspectives on Canadian marine fisheries management. *Edited by* L.S. Parsons and W.H. Lear. Can. Bull. Fish. Aquat. Sci. No. 226. pp. 55–89.

Lear, W.H., Baird, J.W., Rice, J.C., Carscadden, J.E., Lilly, G.R., and Akenhead, S.A. 1986. An examination of factors affecting catch in the inshore cod fishery of Labrador and eastern Newfoundland. Can. Tech. Rep. Fish. Aquat. Sci. No. 1469.

McGrath, P.T. 1911. Newfoundland in 1911. Whitehead, Morris, & Co., London.

Morrissey, J.B. 1993. Biological reference points — some opening comments. *In* Risk evaluation and biological reference points for fisheries management. *Edited by* S.J. Smith, J.J. Hunt, and D. Rivard. Can. Spec. Pub. Fish. Aquat. Sci. No. 120. pp. 1–4.

Mundie, J.H. 1994. The Kemano completion project: an example of science in government. Brief presented to the British Columbia Utilities Commission's Kemano Completion Project Review, Exhibit 487B, Vancouver, B.C.

Mundie, J.H., and Bell-Irving, R. 1986. Predictability of the consequences of the Kemano hydroelectric proposal for natural salmon populations. Can. Water Res. J. **11**: 14–25.

Myers, R.A., and Cadigan, N.G. 1995*a*. Statistical analysis of catch-at-age data with correlated errors. Can. J. Fish. Aquat. Sci. **52**: 1265–1273.

Myers, R.A., and Cadigan, N.G. 1995*b*. Was an increase in natural mortality responsible for the collapse of northern cod? Can. J. Fish. Aquat. Sci. **52**: 1274–1285.

Myers, R.A., Barrowman, N.J., and Hoenig, J.M. 1996*a*. The collapse of cod in eastern Canada: the evidence from tagging data. ICES J. Mar. Sci. **53**: 629–640.

Myers, R.A., Hutchings, J.A., and Barrowman, N.J. 1996*b*. Hypotheses for the decline of cod in the North Atlantic. Mar. Ecol. Prog. Ser. **138**: 293–308.

Myers, R.A., Barrowman, N.J., and Hutchings, J.A. 1997*a*. Inshore exploitation of Newfoundland Atlantic cod (*Gadus morhua*) since 1948 as estimated from mark–recapture data. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1): 224–235.

Myers, R.A., Mertz, G., and Fowlow, S. 1997*b*. The maximum population growth rates and recovery times of Atlantic cod (*Gadus morhua*). Fish. Bull. **95**. In press.

Schouwenburg, W.J. 1994. Submission to the B.C. Utilities Commission public review of the Kemano Completion Project. Brief presented to the British Columbia Utilities Commission's Kemano Completion Project Review, Exhibit 485, Vancouver, B.C.

Shelton, P.A. 1996. Proceedings of the Newfoundland Regional groundfish stock assessment review, April, May, September 1995. Can. MS Rep. Fish. Aquat. Sci. No. 2343.

Sinclair, A.F., and Murawski, S.A. 1997. Why have groundfish stocks declined in the Northwest Atlantic? *In* Perspectives on a fishery collapse. *Edited by* J. Bormenn, B. Nakashima, H. Powles, J. Wilson, and R. Kendall. American Fisheries Society, Bethesda, Md. In press.

Sinclair, A., Chouinard, G., Swain, D., Nielsen, G., Hanson, M., Currie, L., Hurlbut, T., and Hébert, R. 1995. Assessment of the southern Gulf of St. Lawrence cod stock, March 1995. DFO Atl. Fish. Res. Doc. 95/39.

Steele, D.H., Anderson, R., and Green, J.M. 1992. The managed commercial annihilation of northern cod. Nfld. Stud. **8**: 34–68.

Walters, C. 1995. Fish on the line: the future of Pacific fisheries. David Suzuki Foundation, Vancouver, B.C.

Walters, C., and Maguire, J.-J. 1996. Lessons for stock assessment from the northern cod collapse. Rev. Fish Biol. Fish. **6**: 125–137.

Walters, C., and Pearse, P.H. 1996. Stock information requirements for quota management systems in commercial fisheries. Rev. Fish Biol. Fish. **6**: 21–42.

Winters, G.H. 1986. Aide-memoire on 2J3KL assessment: *non gratum anus rodentum*? CAFSAC Res. Doc., Department of Fisheries and Oceans, St. John's, NF.

National Research Council Canada / Conseil national de recherches Canada

Copyright Transfer

ASSIGNMENT OF COPYRIGHT

Ms. No.____________

To: NATIONAL RESEARCH COUNCIL OF CANADA ("NRC") Research Journals

From: ____
____
____
____
(name and address of author signing this form)

This refers to the manuscript entitled: ____
____

written by myself and the following additional author(s): ____
____

for publication in: ____

1. I declare that the list of authors fairly conforms to academic conventions about who should be listed. I declare that the manuscript, or its equivalent, has not been submitted for publication elsewhere. If it is accepted for publication by the National Research Council of Canada, I will ensure that it, or its equivalent, is not submitted for publication elsewhere.

2. I declare that I am (check ONE):

☐ (a) the sole owner of the copyright relating to the manuscript, and → I **assign** to NRC the entire copyright.

☐ (b) a part owner of the copyright, in conjunction with interests held by co-authors or their employers, and → I **assign** to NRC my entire interest in the copyright, and I expect the co-authors to also sign a form like this one.

☐ (c) an agent of my employer with authority to assign the copyright owned by the employer, who is: ______________________, and → I **assign** to NRC, on behalf of my employer, my employer's entire interest in the copyright relating to the manuscript, and I expect the co-authors to also sign a form like this one.

☐ (d) a public servant in Canada (federal, provincial or territorial) or the United Kingdom, so that the copyright is owned by Her Majesty, and → I have obtained the approval of my employer, according to the terms of my employment, to grant NRC **non-exclusive permission** to publish the manuscript and administer the copyright.

☐ (e) a public servant of the United States of America, and subject to the law that creates no U.S. copyright for the manuscript, and → I **assign** to NRC, on behalf of my employer, my employer's entire interest in any copyright that may exist outside the U.S., and I expect the co-authors to sign a form like this one.

3. I understand that my submission of this document does not guarantee publication, and that publication will not occur until **all authors** have provided a copyright transfer. If the manuscript is not published within 2 years after I sign this, the assignment is revoked.

Signed at ______________________________ on ____________________
(City and Province/State) (Date)

____
(Signature)

[*Standard NRC form; alterations not acceptable.*]

Comments on Copyright Transfer
(with extracts from the *Copyright Act*, Revised Statutes of Canada 1985, chapter C-42, as amended)

The publisher is not permitted to publish the manuscript without permission or an assignment of ownership of copyright. For greatest flexibility, and to be prepared to deal with future uses of the published material, the publisher requires ownership.

The owner may assign the right, but that assignment must be in writing:

13.(4) *The owner of the copyright in any work may assign the right, either wholly or partially, and either generally or subject to territorial limitations, and either for the whole term of the copyright or for any other part thereof, and may grant any interest in the right by licence, but no assignment or grant is valid unless it is in writing signed by the owner of the right in respect of which the assignment or grant is made, or by his duly authorized agent.*

The owner may be the author, but in many cases, the owner is the author's employer:

13.(3) *Where the author of a work was in the employment of some other person under a contract of service or apprenticeship and the work was made in the course of his employment by that person, the person by whom the author was employed shall, in the absence of any agreement to the contrary, be the first owner of the copyright, but where the work is an article or other contribution to a newspaper, magazine or similar periodical, there shall, in the absence of any agreement to the contrary, be deemed to be reserved to the author a right to restrain the publication of the work, otherwise than as part of a newspaper, magazine or similar periodical.*

The only exception to taking ownership arises when the manuscript is covered by Crown copyright owned by a Canadian government.

12. *Without prejudice to any rights or privileges of the Crown, where any work is, or has been, prepared or published by or under the direction or control of Her Majesty or any government department, the copyright in the work shall, subject to any agreement with the author, belong to Her Majesty and in that case shall continue for the remainder of the calendar year of the first publication of the work and for a period of fifty years following the end of that calendar year.*

Governments, and in particular the federal government, do not have a simple mechanism for assigning ownership of this particular type of Crown asset. Therefore, when an author is a public servant so that there is Crown copyright in the manuscript, a simple permission to use is acceptable to the publisher, if it is granted by a person with appropriate authority.

Conseil national de recherches Canada
National Research Council Canada
Cession du droit d'auteur

CESSION DU DROIT D'AUTEUR

Document n° ______

Au : CONSEIL NATIONAL DE RECHERCHES DU CANADA («CNRC») - Presses scientifiques
De : ____________________________________
____
____
____
(nom et adresse de l'auteur qui signe le présent formulaire)

La présente cession porte sur le document intitulé : ____________________________
____

rédigé par moi, en collaboration avec l'auteur/les auteurs suivant(s) : ________________
____

aux fins de publication dans :____

1. Je déclare que la liste des auteurs ci-dessus respecte les pratiques usuelles de rédaction savante quant aux personnes dont le nom doit être cité. Je déclare que le document ou son équivalent n'a pas été soumis à quelque autre organisme aux fins de publication. Si le CNRC accepte de publier le document, je m'assurerai que celui-ci ou son équivalent n'est soumis à aucun autre organisme aux fins de publication sans en obtenir la permission préalable du CNRC.

2. Je déclare être (UN SEUL choix) :

☐	(a)	le seul titulaire de droit d'auteur afférent au document,	et →	je **cède** le droit d'auteur intégral au CNRC.
☐	(b)	un titulaire partite du droit d'auteur, de concert avec des coauteurs ou leurs employeurs,	et →	je **cède** ma part du droit d'auteur au CNRC et m'attends à ce que les coauteurs signent une entente comparable.
☐	(c)	un agent de mon employeur ayant l'autorité de céder le droit d'auteur appartenant à l'employeur, nommément : ______________________,	et →	je **cède** au CNRC, au nom de mon employeur, la part entière du droit d'auteur afférent au document appartenant à mon employeur, et m'attends à ce que les coauteurs signent une entente comparable.
☐	(d)	un fonctionnaire du Canada (fédéral, provincial ou territorial) ou du Royaume-Uni, donc le droit d'auteur appartient à Sa Majesté,	et →	j'ai obtenu de mon employeur, en vertu de mes conditions d'emploi, l'autorisation d'accorder au CNRC la **permission non exclusive** de publier le document et de gérer le droit d'auteur.
☐	(e)	un fonctionnaire des États-Unis d'Amérique, donc sujet à la loi qui n'associe aucun droit d'auteur américain au document,	et →	je **cède** au CNRC, au nom de mon employeur, la part entière de quelque droit d'auteur en vigueur ailleurs qu'aux É.-U. appartenant à mon employeur, et m'attends à ce que les coauteurs signent une entente comparable.

3. Je comprends que la soumission du document ne garantit aucunement sa publication et que la publication ne pourra être réalisée tant que **tous les auteurs** n'auront pas signé une cession du droit d'auteur. Si le document n'est pas publié dans les deux années suivant ma signature des présentes, la cession sera automatiquement révoquée.

Signé à ________________________________, le ________________________
(ville et province/état) (date)

____
(signature)

[*Formulaire normalisé du CNRC; aucune modification permise*]

Commentaires sur la cession du droit d'auteur
(accompagnés d'extraits de la *Loi sur le droit d'auteur*, Lois révisées du Canada 1985, chapitre C-42 modifié)

L'éditeur ne peut publier un document sans la permission ou une cession du droit d'auteur. Pour des raisons de souplesse et en vue de l'utilisation future du document publié, l'éditeur doit devenir titulaire du droit d'auteur.

Le titulaire peut céder le droit, mais cette cession doit être faite par écrit :

13.(4) *Le titulaire du droit d'auteur sur une oeuvre peut céder ce droit, en totalité ou en partie, d'une façon générale, ou avec des restrictions territoriales, pour la durée complète ou partielle de la protection; il peut également concéder, par une licence, un intérêt quelconque dans ce droit; mais la cession ou la concession n'est valable que si elle est rédigée par écrit et signée par le titulaire du droit qui en fait l'objet, ou par son agent dûment autorisé.*

Le titulaire peut être l'auteur, mais dans plusieurs cas, le titulaire est l'employeur de l'auteur:

13.(3) *Lorsque l'auteur est employé par une autre personne en vertu d'un contrat de louage de service ou d'apprentissage, et que l'oeuvre est exécutée dans l'exercice de cet emploi, l'employeur est, à moins de stipulation contraire, le premier titulaire du droit d'auteur; mais lorsque l'oeuvre est un article ou un autre contribution, à un journal, à une revue ou à un périodique du même genre, l'auteur, en l'absence de convention contraire, est réputé posséder le droit d'interdire la publication de cette oeuvre ailleurs que dans un journal, une revue ou un périodique semblable.*

La seule exception dans la cession du droit d'auteur est lorsque le document est associé au droit d'auteur de la Couronne, qui appartient au gouvernement du Canada .

12. *Sous réserve de tous les droits ou privilèges de la Couronne, le droit d'auteur sur les oeuvres préparées ou publiées par l'entremise, sous la direction ou la surveillance de Sa Majesté ou d'un ministère du gouvernement, appartient, sauf stipulation conclue avec l'auteur, à Sa Majesté et, dans ce cas, il subsiste jusqu'à la fin de la cinquantième année suivant celle de la première publication de l'oeuvre.*

Les gouvernements, en particulier le gouvernement fédéral, ne disposent pas d'un mécanisme simple de cession de droit d'auteur pour ce genre de biens de la Couronne. C'est pourquoi lorsqu'un auteur est un fonctionnaire et que, par conséquent, le droit d'auteur appartient à la Couronne, une simple permission d'usage est suffisante pour l'éditeur, pour autant que celle-ci ait été octroyée par une personne jouissant de l'autorité nécessaire pour ce faire.

National Research Council Canada	Conseil national de recherches Canada
NRC · CNRC	
Research Journals	***Revues scientifiques***
† Biochemistry and Cell Biology	† Biochimie et biologie cellulaire
• Canadian Journal of Botany	• Revue canadienne de botanique
• Canadian Journal of Chemistry	• Revue canadienne de chimie
• Canadian Journal of Earth Sciences	• Revue canadienne des sciences de la Terre
‡ Canadian Journal of Fisheries and Aquatic Sciences	‡ Journal canadien des sciences halieutiques et aquatiques
† Canadian Journal of Forest Research	† Revue canadienne de recherche forestière
• Canadian Journal of Microbiology	• Revue canadienne de microbiologie
† Canadian Journal of Physics	† Revue canadienne de physique
‡ Canadian Journal of Physiology and Pharmacology	‡ Revue canadienne de physiologie et pharmacologie
• Canadian Journal of Zoology	• Revue canadienne de zoologie
† Canadian Journal of Civil Engineering	† Revue canadienne de génie civil
• Genome	• Génome
† Canadian Geotechnical Journal	† Revue canadienne de géotechnique
† Environmental Reviews	† Dossiers environnement
‡ Electronic version available	**‡ Disponible en version électronique**
† Electronic version available in 1997	**† Disponible en version électronique en 1997**
Subscription Office, M-55 NRC Research Press National Research Council Canada Ottawa, ON K1A 0R6 Canada Tel.: 613-993-9084 Fax.: 613-952-7656 E-mail: research.journals@nrc.ca **URL: http://www.nrc.ca/cisti/journals/rj.html**	Bureau d'abonnements, M-55 Presses scientifiques du CNRC Conseil national de recherches du Canada Ottawa, ON K1A 0R6 Canada Tél. : 613-993-9084 Télécopieur : 613-952-7656 Courrier électronique : research.journals@nrc.ca **URL : http://www.nrc.ca/cisti/journals/rj.html**

Climate Change and Northern Fish Populations

(Canadian Special Publication of Fisheries and Aquatic Sciences 121) • 768 pages

Monograph/Monographie

Editor: Richard J. Beamish

Canada $70.00 • Other countries $70.00 (U.S.) (ISBN 0-660-15780-2; ISSN 0706-6481; NRCC No. 38663

These proceedings summarize some of the recent studies of the relationships among climate, the aquatic environment, and the dynamics of fish populations. The studies are mostly from the North Pacific Ocean, but there are reports of investigations from the North Atlantic Ocean and from fresh water. The various papers include numerous examples of the relationships between fish abundance trends and the environment.

To order copies, complete the order form below

Please send me____copies of *Climate Change and Northern Fish Populations*

$70 ea.* __________

Make cheque or money order payable to "Receiver General for Canada, credit NRC" and send to:

Monograph Orders, Building M-55
NRC Research Press
National Research Council Canada
Ottawa, ON K1A 0R6, Canada

*Canadian customers please add 7% GST. In Quebec please add a further 6.5% QST to the total price including GST. Non-Canadian orders payable in U.S. funds.

Rédacteur : Richard J. Beamish

Canada $70.00 • Autres pays $70.00 (U.S.) (ISBN 0-660-15780-2; ISSN 0706-6481; NRCC No. 38663

Les actes rendent compte de quelques-unes des plus récentes études sur les relations entre le climat, l'environnement aquatique et la dynamique des populations de poissons. Bien que la plupart des études aient été effectuées dans le Pacifique nord, certaines relatent des recherches dans l'Atlantique nord et en eau douce. Les divers articles contiennent de nombreux exemples des relations entre les tendances de l'abondance des poissons et l'environnement.

Pour commander des exemplaires veuillez remplir le bon de commande ci-dessous

Veuillez me faire parvenir_____exemplaire(s) de *Climate Change and Northern Fish Populations*

70 $ chac.* __________

Libellez le chèque ou mandat au «Receveur général du Canada, crédit du CNRC» et faites-le parvenir à :

Monographies, édifice M-55
Presses scientifiques du CNRC
Conseil national de recherches Canada
Ottawa, ON K1A 0R6, Canada

*Clients canadiens, veuillez ajouter 7 % pour la TPS. Au Québec, veuillez ajouter 6,5 % de plus pour la TVQ au montant total y compris la TPS. Pour les commandes de l'étranger, les tarifs sont en dollars américains.

PLEASE PRINT / EN LETTRES MOULÉES

Visa ☐ MasterCard ☐ Expiry date/Date d'expiration month/mois ____ year/année ____

Account No. / N° de compte ☐☐☐☐☐☐☐☐☐☐☐☐☐☐☐☐

Name/Nom ____________________

Signature ____________________

Address / Adresse ____________________

City / Ville ____________________ Province/State / Province/État ____________________

Postal Code/Zip Code / Code postal ____________________ Country / Pays ____________________

Telephone No. / N° de téléphone ____________________ Fax No. / N° de télécopieur ____________________

Electronic mail / Courrier électronique ____________________

NRC · CNRC

Contents (concluded) / Table des matières (suite et fin)

Yoshiro Watanabe, Yoshioki Oozeki, and Daiji Kitagawa 1067–1076 Larval parameters determining preschooling juvenile production of Pacific saury (*Cololabis saira*) in the northwestern Pacific

Douglas P. Swain 1077–1087 Sex-specific temperature distribution of American plaice (*Hippoglossoides platessoides*) and its relation to age and abundance

M.J. Paterson, D. Findlay, K. Beaty, W. Findlay, E.U. Schindler, M. Stainton, and G. McCullough 1088–1102 Changes in the planktonic food web of a new experimental reservoir

Robert G. Fechhelm, James D. Bryan, William B. Griffiths, and Larry R. Martin 1103–1110 Summer growth patterns of northern Dolly Varden (*Salvelinus malma*) smolts from the Prudhoe Bay region of Alaska

P. Pepin and J.T. Anderson 1111–1120 Scale-dependent variations in the precision of larval fish abundance estimates: a study of *Sebastes* sp. on Flemish Cap

J. Zheng, M.C. Murphy, and G.H. Kruse 1121–1134 Analysis of harvest strategies for red king crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska

Brian G. Fraser and D. Dudley Williams 1135–1141 Accuracy and precision in sampling hyporheic fauna

M. Jake Vander Zanden, Gilbert Cabana, and Joseph B. Rasmussen 1142–1158 Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}N$) and literature dietary data

Sean P. Cox and Scott G. Hinch 1159–1165 Changes in size at maturity of Fraser River sockeye salmon (*Oncorhynchus nerka*) (1952–1993) and associations with temperature

David R. Stanley and Charles A. Wilson 1166–1176 Seasonal and spatial variation in the abundance and size distribution of fishes associated with a petroleum platform in the northern Gulf of Mexico

Howard P. Gross, Wayne A. Wurtsbaugh, Chris Luecke, and Phaedra Budy 1177–1189 Fertilization of an oligotrophic lake with a deep chlorophyll maximum: predicting the effect on primary productivity

PERSPECTIVES PERSPECTIVES

S.R. Kerr and R.A. Ryder 1190–1197 The Laurentian Great Lakes experience: a prognosis for the fisheries of Atlantic Canada

Jeffrey A. Hutchings, Carl Walters, and Richard L. Haedrich 1198–1210 Is scientific inquiry incompatible with government information control?

Editorial iii **Éditorial** iii

National Research Council Canada
Ottawa, Canada
K1A 0R6

Conseil national de recherches Canada
Ottawa, Canada
K1A 0R6

Canadian Journal of Fisheries and Aquatic Sciences

Volume 54, Number 5, May 1997

Journal canadien des sciences halieutiques et aquatiques

Volume 54, numéro 5, mai 1997

ARTICLES ARTICLES

A.L. Jensen **987–989** Origin of the relation between K and L_{inf} and synthesis of relations among life history parameters

Donald R. Gunderson **990–998** Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes

Harold E. Welch, Timothy D. Siferd, and Philip Bruecker **999–1005** Marine zooplanktonic and benthic community respiration rates at Resolute, Canadian high Arctic

Thomas A. Johnston **1006–1014** Within-population variability in egg characteristics of walleye (*Stizostedion vitreum*) and white sucker (*Catostomus commersoni*)

Kedong Yin, Paul J. Harrison, and Richard J. Beamish **1015–1024** Effects of a fluctuation in Fraser River discharge on primary production in the central Strait of Georgia, British Columbia, Canada

Jason B. Dunham and Gary L. Vinyard **1025–1030** Relationships between body mass, population density, and the self-thinning rule in stream-living salmonids

Craig A. Stow, Leland J. Jackson, and James F. Amrhein **1031–1038** An examination of the PCB:lipid relationship among individual fish

M.H.G. Berntssen, F. Kroglund, B.O. Rosseland, and S.E. Wendelaar Bonga **1039–1045** Responses of skin mucous cells to aluminum exposure at low pH in Atlantic salmon (*Salmo salar*) smolts

Uwe Borgmann and Warren P. Norwood **1046–1054** Toxicity and accumulation of zinc and copper in *Hyalella azteca* exposed to metal-spiked sediments

Uwe Borgmann and Warren P. Norwood **1055–1063** Identification of the toxic agent in metal-contaminated sediments from Manitouwadge Lake, Ontario, using toxicity–accumulation relationships in *Hyalella azteca*

A.F. Youngson, A.I. Mitchell, P.T. Noack, and L.M. Laird **1064–1066** Carotenoid pigment profiles distinguish anadromous and nonanadromous brown trout (*Salmo trutta*)

Continued on inside back cover / Suite au verso

Canada

Printed in Canada by / Imprimé au Canada par
University of Toronto Press Inc.
Typesetting by / Typographie par
NRC Research Press / Presses scientifiques du CNRC

0706-652X(199705)54:5;1-0